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Mémoire

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Impact of incoming light quantity on plant growth strategy and assimilate partitioning during crop establishment

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Summary

1 - Introduction

Rice is life for almost half the planet’s population. Each day, millions of poor around the world depend on rice as staple food and employment. The majority of all rice produced comes from China, India, Indonesia, Bangladesh, Viet-Nam and Thailand with asian farmers still accounting for 92-percent of the world's total rice production. Today, rice is grown and harvested throughout the world, wherever conditions allow its growth, namely in warm moist climates. Rice farming systems are diversified, from dry temperate regions to flooded cultures in the tropics, from rainfed lowland in Africa or South America to low temperature upland in Madagascar or Asia, in deepwater or flood-prone environments where the water depth may exceed 5 meters. In the year 2003, the world produced about 589 million tons of paddy rice and most of it, about 534 million tons, were grown in Asia (1). By 2025, there will be 650 million rice consumers simply in Asia. Asia’s farmers will have to produce millions of tons of extra rice, using less land, less labor and less water. Competition for these vital resources is already intense, forcing rice farmers to produce much more with less.

The first rice specie (*Oryza sativa*) was grown in East and South Asia as long as 15,000 years ago, when people began to settle in river deltas and domesticated wild rice. For thousands of years, humans have shuffled genes by breeding and selection in order to improve yield through familiar domestic varieties of this grass species. This process of selection is at the origin of a rich genetic inheritance of almost 140 000 varieties of *Oryza sativa* (Jeanguyot, 2002). Considerable progress has been accomplished in taste, nutritional value and productivity, notably during the "Green Revolution" which took place between 1960 and 1970. The aim of this revolution was to intensify the crop production with double-cropping systems and improved genetic materials. The International Rice Research Institute (IRRI), Los Baños, Philippines was an important actor of this revolution since it was founded in 1960 and has been helping poor rice farmers and consumers by introducing new technologies into rice fields in Asia from excellent scientific research. However, the Green Revolution has also known its failures, and we can no longer count on universal distribution of a few "high yield" varieties. Rice farming systems are now facing soil N pollution, CH4 emission, pesticide abuses and all of these issues may have a direct impact on human health. A highly integrated scientific approach is required to improve rice yields and reduce inputs. The advances in agronomy, the world population explosion, the loss of arable land and the threat of climate change require a new revolution: designing and creating rice genotypes specially adapted to well defined growing conditions and adapting crop management to the characteristics of the genotypes to increase profit for farmers and to be more friendly with the environment.

2 - Context

During the last 10 years, new tools in biotechnology, genome research, biomathematics and ecophysiology have offered new opportunities to solve many of the problems that are faced by farming systems. In particular, these tools would allow to design improved genotypes characterized with high resources use efficiency at a time when agriculture is required to be more profitable with farmers, less competitive with industries and cities for water use and more friendly with the environment. Rice is the cereal considered as the model plant of the *Poaceae*, not only in the field of genomics but also of phenological development and of adaptative response to environmental conditions (Jun *et al.*, 2002). Rice has the smallest genome of all the cereals (430 million nucleotides), (Sasaki and Burr, 2000; Eckardt, 2000; Arumuganathan and Earle, 1991) and can serve as a model genome for monocotyledons, in the same way as Arabidopsis thaliana is the one for dicotyledons, Preliminary comparisons between different cereal genomes revealed large blocks of homologous genes whose sequence is relatively well conserved. This phenomenon, known as synteny, makes then rice a good entry point for characterizing the genes of other cereals (Bevan and Murphy, 1999; Wang *et al*., 1995; Gale and Devos, 1998; Messing and Llaca, 1998; Goff, 1999), and associating them with various agronomic traits through ecophysiological modelling. The scientific and technological means are thus met to conceive and realize rice ideotypes to contrasted growing conditions. These ideotypes, most adapted phenotypes for optimal performance regarding the characteristics of their environments (Mutsaers, 1999), would be the result of well designed genotypes from appropriate gene combination for potential agronomic performance. If the genotype is fixed, the phenotype is described by all the morphological, physiological, ethologic and ecological aspects of the plant (David, 1989). The ambitious scientific aim here consists in relating the variety of the phenotypes generated by a single genotype to the characteristics of the growing conditions, or in short to characterize the complexity of the interactions genotype *x* environment (G*x*E) through the phenotypical plasticity. This requires the elaboration of an ecophysiological model used as a tool to integrate biological, biophysical and physiological plant processes and to predict plant behavior according to growing conditions from constitutive and inductive traits.

In 2002, the Oryzon Project was initiated by CIRAD, Montpellier, France, in collaboration with other research institute, to establish an integrated continuum of research from molecular genetics to agronomy in order to gather scientists from different disciplines towards a common objective of ideotypes creation. Researchers of the Research Unit Ecotrop (CIRAD) are currently developing a growth plant model, Sarrah-meristem (Dingkuhn, 2005), that aims in predicting the phenotypical plasticity of cereals, considering first rice, pearl millet and sorghum. This model, descriptive and mechanistic, aims at simulating plant growth and development in response to the variability of the environment with regards to the meristem activity conditioning the installation of plant architecture (Prusinkiewicz, 2004) and to the carbohydrates demand of the active plant organs conditioning carbohydrates partitioning. Within the framework of the Oryzon Project, I carried out my Master training course at IRRI with the main objective to analyze the phenotypical plasticity of an improved popular high-yielding genotype during the vegetative and reproductive phases in response to contrasted incoming radiation periods set up at different crop stages. A similar experimentation, but focusing rather on physiological relationships at the leaf level, was carried out at the same time and on the same genotype in a controlled environment in Montpellier (Luquet and Martin).

3 - Literature

Characterizing the chronology of elementary processes, that drive plant growth and development, and the range in variation of these processes is essential in order to take into account the impact of genetic variability and change in growing conditions on crop growth. This approach implies to determine, in a range of environments, the succession of each event driving plant development and to quantify the growth dynamics of plant organs with plant age in order to characterize phenotypical plasticity and its determinism. Partitioning of available carbohydrates would then be driven according to the potential demand of the competitive sinks and the hierarchy amongst them to access these carbohydrates. This concept has been successfully used in previous studies (DeJong and Grossman, 1994; Heuvelink, 1996; Tabourel-Tayot and Gastal, 1998). This has also been undertaken to model the rate in tiller senescence in sorghum when competition for assimilate became critical (Lafarge and Hammer, 2002): the rate of decrease in potentially fertile tiller number per plant was related to the ratio of realised to potential leaf area growth during the period of decrease. The potential growth in leaf area (demand) was estimated from the leaf area that would be produced between two observations if all potentially fertile tillers were to continue their development. Adapting on rice this dynamic approach during the vegetative and reproductive phases would then be a great challenge and improvement in moving towards designing cereal ideotypes for specific field conditions. This requires, as a first step, to characterise plant phenology, the dynamics of leaf and tiller production, and of the partitioning of carbohydrates towards leaf blades, sheaths, internodes, panicles and reserves and their variability in contrasted incoming radiation.

3.1 Assimilates partitioning

Carbohydrate gain in the rice plant is partitioned between formation of new structures (leaves, tillers, roots, internodes, spikelets and grain), changes of actual structures (leaf thickness, stem and root diameter, grain filling) and requirements for maintenance and growth respiration (Gifford et al., 1984). Contrasted partitioning across varieties leads to commonly classify them into two main groups, and their intermediates, according to their vegetative growth strategy: one of plants that colonise rapidly the available space and resources by developing lots of tillers with thin leaves, stems and roots, and the other of plants that rather invest in reserves and mechanical resistance by developing few tillers with thick leaves, stems and roots (Lafitte and Travis, 1984; Peng et al., 1999; Siband, unpublished data). The direction of assimilate translocation is primarily regulated by the relative sink strength of an organ. Plant development might be limited by source availability and by plant regulatory factors, depending on the growing conditions and plant stage. For irrigated rice, where in most cases the highest tillering plants are the one with the highest grain yield (Wu et al., 1998), these different strategies in plant growth lead to contrasted patterns in assimilate partitioning, mainly in terms of tiller production, assimilate storage and remobilization.

3.2 Tiller emergence regarding growth environment

Tiller production has generally been analysed on high tillering species and rice cultivars differ greatly in tiller ability (Maruta and Matsushima, 1965; Yoshida, 1981). Tillering is one of the most important traits of rice considering adaptation to various types of environments, compensation because of contratsted growing conditions and crop ability to produce grain (Counce and well, 1991; Miller at al., 1991; Gravios and Helms, 1992). It was observed that tiller emergence was driven first by tiller site formation at the base of every leaf associated with leaf production, and secondly by the number of buds that develop into tillers. The concept of site filling, expressed as number of new tillers per tiller per phyllochron (time between appearance of two consecutive leaves), was introduced by Davies (1974) and generalized by Neuteboom and Lantiga (1989). Tiller emergence is commonly affected by plant density (Counce and Well, 1991; Schnier et al., 1990a) that directly affects plant access to light and nutrients (Liang et al. 1986). As plant density increases, the proportion of secondary and tertiary tillers decreases (Hoshikawa, 1989; Miller et al., 1991). Shading inhibits tiller production and enhances tiller mortality (Matsushima, 1970; Ong et Marshall, 1979; Mc Master et al., 1987; Yamamoto et al., 1995; Caton et al., 1997). In conditions where tillering is affected neither by water stress nor by nitrogen stress, several authors have suggested that plant carbon balance, and in particular the availability of assimilates, drives tiller production (Mitchell, 1953; Ong and Marshall, 1979). This was observed in wheat, rice, barley, ryegrass and sorghum (Friend, 1965; Honda and Okajima, 1970; Kirby and Faris, 1972; Ong and Marshall, 1979; Gerik and Neely, 1987), even though light quality was reported to affect duration of tiller emergence (Casal et al., 1986; Gautier et al., 1995). It appears that this possible response to light quality acts mostly as an early perception of assimilate shortage prior to any appreciable mutual shading and depletion of assimilate resources (Deregibus et al., 1985; Ballaré et al., 1987). In contrast, from the assumption of a trophic regulation of tiller dynamics in the canopy, it has been reported that the demand is completed and new tillers are formed, and emerge on a regular pattern, as soon as the supply exceeds the demand. When the supply cannot meet the demand, emergence of new tillers is stopped (Penning de Vries et al., 1989; Schnier et al., 1990; Drenth et al., 1994).

Tiller emergence rate, however, has been in most cases related to leaf appearance rate (Davies and Thomas, 1983, Klepper et al., 1982; Skinner and Nelson, 1992; Kirby, 1995; Sugiyama, 1995), which determines the rate of tiller site production (Davies, 1974; Vavies and Thomas, 1983; Zarrough et al., 1984). Thermal time-based leaf appearance rate of sorghum was reported to be very stable in a wide range of climate conditions (Lafarge and Tardieu, 2002) and to be similar on the different axes of the tillering plants at any time (Masle-Meynard and Sébillotte, 1981; Klepper et al., 1982; Kirby, 1995). This relationships between leaf and tiller emergence implies that the growing conditions affecting leaf emergence rate are affecting tiller production similarly, which could be valid only at early stage. The onset of a reduction in tiller emergence in response to detrimental environmental conditions or increasing competition for light interception has often been analysed in terms of deviation from the potential linear relationship in high tillering species (Kirby et al., 1985; Bos and Neuteboom, 1998; Gautier et al., 1999). A common linear relationship was observed between relative tillering rate (RTR) and relative shoot growth rate (RGR), as for rice and tall fescue (Schnier et al., 1990; Sugiyama, 1995), including the period when tiller emergence departed from that in the control plots. Differential tillering rates and leaf area development among varieties and environment were therefore related to dry matter acquisition, based on a common relationship for morphologically and phenologically different materials (Dingkuhn at al., 1991). Because of its characteristics, this relationship, however, considers that tillering is the only sink for shoot carbohydrates during the whole period when this is applied. This does not appear relevant, particularly when new sinks appear in the plant like internodes and panicles. The maximum tiller number per plant is not predicted in most crop models and the cessation in tiller emergence is commonly fixed at a certain growth stage such as panicle initiation or start in internode elongation (Graf et al., 1990; Gao et al., 1992; Miller et al., 1993). Rather, the cessation in tiller emergence could be predicted according to a critical value of LAI (Zhong et al., 2002; Lafarge and Hammer, 2002) for which change in light quality inside the canopy may affect tiller production.

3.3 Internode and panicle: major sink for assimilate partitioning

Partitioning of shoot assimilate between leaf, stem and head with thermal time was stable in sorghum across plant densities from emergence until anthesis at both plant and culm level (Lafarge and Hammer, 2002) but was variable regarding rice cultivars and their growth strategy (Asch et al., 1999). Elongating internodes become a major sink for leaf assimilate during vegetative development and a disparity in assimilate distribution to the internode can cause differences in final length (Morrison et al., 1994), as this was observed when shading (Fournier and Andrieu, 2000): the onset and the rate of the linear elongation phase was delayed, but its duration was not affected. Internodes are important site for storage of non-structural carbohydrates before flowering if occurrence of any period of stress (de Raïssac, 1992; Cruz-Aguado et al., 2000), or also at the beginning or end of grain filling if the grain sink capacity is not strong enough (Rajcan and Tollenaar, 1999). The same observation is also valid after an early stoppage of grain growth due to shading at early grain filling (Kobata et al., 2000). Preferential partitioning of assimilate carbon into the panicle occurred under a low irradiance period at the beginning of grain filling and priority of superior spikelets intensified (Okawa et al., 2003).

3.4 Carbohydrate remobilization

Carbohydrate remobilization from vegetative sink to grain during ripening has been well studied and reflects the degree to which sink activity is matched by source supply (Yoshida, 1980).The supply of assimilate to reproductive sinks may come from the sheath and from several leaves, depending on their age and position and on the reproductive status of the plant. Shading during the first period of grain filling in rice affected grain and even straw dry weight with time, whereas no effect was observed on senescence (Kobata et al., 2000). Carbohydrates remobilization from straw is expected to have shortened the gap between control and shaded plants in terms of grain yield. It is also suggested that reduction in straw dry matter and N retention in leaves during shading accelerated the photosynthetic rate after shading removal. Carbohydrate remobilization during vegetative development did, however, receive less credit and few significant studies are available regarding variation in specific leaf area.

3.5 SLA: an approach to modeling growth strategies

Specific leaf area (SLA), defined as the ratio between leaf blade area and its dry weight, was introduced as a concept to determine the physiological cost to produce leaf area (Evans, 1972) and to address how leaf structure is affected by growing conditions. It is widely used to distinguish growth strategies of species favorable to space colonization from those favorable to reserves investment (Poorter and De Jong, 1999). As a consequence, rice genotypes characterized with high SLA are considered to be highly competitive against weeds (Dingkuhn et al., 1999). It is reported that genotypic SLA has a much greater effect on LAI than assimilate partitioning ratio, light extinction coefficient and mean leaf tip elevation angle. In the same way, hybrid rice presented, during the vegetative phase, higher leaf area growth rate and crop growth rate, possibly due to thinner leaf blades rather than higher tillering rate (Laza et al., 2001). In most modelling approaches (CERES; Van Henten, 1991; Heuvelink, 1999; Lafarge and Hammer, 2002), increase in plant leaf area on a given day is related to carbon gain on that day, proportion of carbon allocated to leaf blades and plant SLA. This approach implies that SLA is constant for a genotype or that its changes with plant stage and environmental conditions are predicted in a simple way (Marcelis et al., 1998) but this cannot take into account the impact of day-to-day variation in growing conditions on SLA. However, systematic tiller removal in sorghum plants promoted a significant decrease in specific leaf area with decreasing density, as the plant was unable to compensate by producing bigger leaves (Lafarge and Hammer, 2002). Similarly, Heuvelink and Buiskool (1995) measured a decrease in specific leaf area of tomato plants when assimilate demand, but not assimilate supply, was reduced by fruit and truss pruning. It is therefore relevant to quantify how SLA is changing with plant stage under contrasted incoming radiation and how this could be taken into account in a modeling approach.

4 – Problematic

Improvement of radiation, water and nutrient use efficiency in favorable rice growing environments requires to grow more efficient genotypes with more appropriate crop management. This genotype efficiency depends on the phenotypical plasticity of the plant and its ability to react to the environmental conditions by modulating its development and its carbohydrate partitioning strategy. Phenotypical plasticity during the vegetative and reproductive phases is possible thanks to architectural, morphological and physiological features such as crop duration and developmental program, carbohydrates partitioning for plant height, tillering and plant reserves, and reserves mobilization from stored carbohydrates and senescent organs. Analyzing, quantifying and modeling this plasticity would allow the development of a process based crop modeling, considering the elementary mechanisms of the individual plant growth in the canopy, and the identification of adapted phenotypes to particular growing conditions. In particular, driving the relative tillering rate with the relative growth rate requires that the partitioning coefficient of the total dry matter increase to leaf blades and leaf sheath are constant during the whole period when this relationship is used. It was proposed to identify, under contrasted conditions, invariants from plant growth and development and to determine priority for carbohydrates partitioning regarding plant growth stage when the source is not able to meet the demand anymore. The source for plant carbohydrates was limited in this study through several shading periods applied in the field at different crop growth stages and plant growth and development was then compared with data obtained under natural incident radiation. Constitutive and environment-inductive process could then be identified. This source limitation was expected to affect the plant dry matter accumulation in response to the reduction in light interception, and subsequently tiller dynamics and assimilate partitioning. Sensitivity of the phenology and priority between sinks when internal competition for carbohydrates increased were also evaluated according to the stage of development.

The specific objectives of this study were:

1. To quantify the variation in plant height, plant phenology (key stages and leaf number), tiller dynamics, organ morphology and dry matter partitioning between leaf blades, sheaths, internodes and panicle in response to low incoming radiation periods during the vegetative and reproductive phases;

2. To evaluate the sensitivity of the above variables to low incoming radiation and the priority between the competitive sinks of the plant regarding the plant growth stage;

3. To identify the main components responsible for the phenotypical plasticity of the plant;

5 - Materials and methods

5.1 Site description

Field experiments were conducted during the dry season 2005 in the tropical environment of the IRRI farm, Los Baños (14°11'N, 121°15'E, 21 m altitude), Philippines. The soil was an Andaqueptic Haplaquoll consisting of 58 % clay, 33 % silt, and 9 % sand with $pH_{(H2O)}$ of 6.6, $pH_{(CaCl2)}$ of 6.5, 1.71 % organic C, 0.174 % total N, and 38.23 meq $100g^{-1}$ cation exchange capacity.

5.2 Plant growth and design

5.2.1 Design of the experimentation, plant materiel and growing conditions

IR64 plants were grown in the field under six different conditions of radiation before heading in a randomized complete block design with four replicates (24 plots) *(Annex 2 and 3)*. IR64 is a popular improved inbred line with high yield potential, superior cooking quality and is resistant to brown planthopper, green leaf hopper, blast and bacterial blight. Seeds were soaked for 24 hours, drained and incubated for another 24 hours in order to promote germination. Pre-germinated seeds were sown on February 13 at a rate of 3000 seeds m^{-2} in a well levelled wet-bed nursery. Fifteen day old seedlings were pulled out from the nursery and transplanted on February 28 in the main field at a density of 25 plants m^2 in plots of 6.5 m by 8.5 m large (55.25 m^2). Hill spacing was 0.2 by 0.2 m with one seedling per hill. Prior to transplanting, the main field was flooded, the soil was harrowed and puddle, and water was maintained at a sufficient level to cover the soil and was used as a guide to level the field. Shading was imposed in the field during nine consecutive days at four distinct growth stages: (i) from early to mid-tillering, 7 to 18 days after transplanting (DAT) (Rad1), (ii) from mid to max tillering, 21 to 30 DAT (Rad2), (iii) from few days prior to panicle initiation to early internode elongation, 35 to 44 DAT (Rad3) and (iv) from early to mid internode elongation, 44 to 53 DAT (Rad4). In addition, shading was imposed from early tillering to mid internode elongation 7 to 53 DAT (Rad5). All these situations were checked against a control plot without shading (Rad0). Black nets (6 m x 8 m, 48 m^2) designed to decrease incoming radiation by 70% were strung 30 cm above the canopy level in each of the plot at a time when shading treatment was required. They were adjusted every 4 to 5 days. Measurement of the hemispheric transmittance (Uni003 Unispec spectrometer, PP Systems, Amesbury, MA, USA) of the net in the whole range of the photosynthetic active radiation was carrying out to check if the quality of the transmitted light was modified. The net was placed outdoor 10 cm above the sensor and 3 reps were collected for each wavelength. The red/far-red ratio of the incoming radiation below the net was not modified and was 0.999 of the ratio of the incident radiation. In addition to these treatments, one side of the control plots (Rad0) were thinned to half the initial density (12.5 hills m-2) on the same day as the net was set up in Rad2, Rad3 and Rad4 and designed as Iso 2, Iso3, and Iso4, respectively: every second plant in the first six rows of one side of each plot Rad0 was removed. Because growth of plants from Iso2 did not depart significantly from that of the control plot, and because plants from iso3 were significantly different from control plants on the first day when the treatment was established, possibly because they were sampled too close to the border, the data of these two treatments were presented in the present study.

5.2.2 Crop management

Phosphorus (50 kg P ha^{-1} as single superphosphate), potassium (50 kg K ha^{-1} as muriate of potash) and zinc (5 kg Zn ha^{-1} as zinc sulfate heptahydrate) were applied and incorporated in all the plots one day before transplanting. N application, in a form of urea, was driven to ensure optimal N inputs during the crop cycle. Twice a week, leaf N content was estimated with SPAD (Chlorophyll meter SPAD-502, Minolta Co Ltd, Japan) measurements in order to avoid any N toxicity or deficiency. It was checked that SPAD values were not lower than 35 and higher than 40 (Peng *et al.*, 1996). N application was then done accordingly. As a result, a total of 120 kg N ha^{-1} was applied in four splits (40 kg N ha^{-1} as basal, 40 at mid-tillering and 40 kg between panicle initiation and flowering) in all plots except those corresponding to Rad5, that did not receive the last application of Nitrogen. Green Leaf N content was subsequently analysed in the lab, following the protocol of Nelson and Sommers (1980). Data on Fig. 1 show that leaf N content in all plots and throughout the plant cycle was never deficient nor toxic: it was higher than 2.5% at tillering and than 2.0% at flowering and lower than 4.5% at all times (Dobermann and Fairhurst, 2000). Standard cultural management practices were followed. The field was flooded two days after transplanting and a floodwater depth of 5 cm was maintained until 10 days before physiological maturity when the field was drained. Pesticides and herbicides were used to avoid plant damages and yield loss. Weeds were controlled by applying Soft-it (pretilachlor) 2 DAT. Subsequent weeding was done manually when required (36 and 45 DAT). Pesticides as Molliscide (niclosamide 250g h^{-1}) was sprayed 2 days before transplanting to control snails, Furadan (3.5% carbofuran) granules were applied 2, 11, 30, 44 and 53 DAT to control whorl maggots, and dimotrin (15 DAT), cymbush (18 DAT), Regent (26 DAT) and Opsim and Dimo (32 DAT) were also applied.

5.3 Climatic measurement

Incident solar radiation, Rg (GS1 dome solarimeter, Delta-T Devices, Cambridge, UK), air temperature, T_a, and relative humidity, rH, in a ventilated cylinder (HMP35A, Vaisala Oy, Helsinki, Finland), were measured 2 m above ground level. Air temperature and relative humidity in a ventilated cylinder was also measured with an extra sensor in a Rad5 plot below the net and 10 cm above the canopy level. Soil temperature (T_s) was measured at 20 mm depth below the soil surface with 10 thermocouples (compensation cable for type T thermocouple, Chauvin Arnoux, Pyro-Contrôle, Vaux-en-Velin, France) in 5 random locations in plots with nets and 5 other in plots without net. From 44 DAT, time when the plant meristem was observed to be located above the water level in response to internodes elongation, until panicle emergence, 6 of the 10 thermocouples were removed from the soil and strung to main tillers at meristem level to measure the canopy temperature at the meristem height (T_c). The position of these thermocouples was adjusted regularly. Radiation in the range 0.4-2.2 µm was measured at ground level by placing 19 tube solarimeters (Type TSL, Delta-T Devices, Cambridge, UK) of 1 m long 0.05 m above ground level from 8 to 73 DAT. Three tubes were set up in RAD0, 3 in RAD1, 3 in RAD2, 2 in RAD3, 2 in RAD4 and 4 in RAD5. Two additional tubes, placed in Rad1 and Rad2 at the beginning of the experiment, were moved to Rad3 and Rad4 on 35 and 44 DAT, respectively. Three more solarimeters were placed just above the canopy level, two in Rad0 and one in Rad5, to be used as reference. All the solarimeters were oriented in the same way diagonally across three rows so that the ends of the tubes were both midway between rows and levelled by use of built-in levelling bubble. The glass of the solarimeter was cleaned regularly with alcohol and dead leaves were removed weekly from plants around the tube solarimeters, so that the radiation transmitted was dependent on green leaves only. Prior to installing the solarimeters in the field, they were calibrated by positioning the whole set during seven consecutive days in an area free from shading, choosing one of them as a reference and determining correction factors for the others. All data were measured every minute and averaged and stored every 20 minutes in a data logger (CR10X, Campbell Scientific, Shepshed, Leicestershire, UK). Daily cumulative global radiation was calculated as the sum of the 20-min period Rg of the whole day.

Daily cumulative global radiation varied from 5 up to 25 MJ m^{-2} from transplanting to flowering, with an apparent higher average after 35 DAT (Fig. 2a). At the same time, minimum air temperature (Tn) varied from 20 to 25 °C and maximum (Tx) from 26 to 35 °C, with higher temperature close to flowering (Fig. 2b). Air vapour pressure deficit (VPDa) was calculated as the difference between saturated pressure of water at actual air temperature minus that at air dew point temperature. Mean day-time VPDa was calculated from 8 am until 5 pm every day until flowering. Mean day-time VPDa was never higher than 2.2 kPa (Fig. 2c) and even instantaneous VPDa was never higher than 2.6 kPa (data not shown).

Daily thermal time (δTT) was simply calculated by daily integration of the meristem temperature minus a threshold temperature of 12 °C. Meristem temperature was assumed to correspond to soil temperature (T_s) until start in internodes elongation (time when plant meristem was above water level) and to canopy temperature at meristem height until heading (T_{ci}) and at panicle height thereafter (T_{co}) (Jamieson *et al*., 1995; Lafarge *et al*., 1998). The threshold temperature was derived from studies on photo-thermal models of rice growth duration set up for various varieties, where the lowest temperature limiting rice development was 12 °C for *indica* rice (Gao *et al*., 1987). The common model using a broken linear function of temperature to calculate thermal time, considering an 'optimal' and a 'maximal' temperature (Alagarswamy *et al*., 1986; Ritchie and NeSmith, 1991; Hammer *et al*., 1993) was not considered appropriate here, and a single integration was used as VPDa was always lower than 2.5 kPa (Lafarge *et al*., 1998). Thermal time (TT) was then calculated by accumulating δTT from transplanting.

The fraction of incident radiation intercepted in the plot *x* (Fi_x) was determined for each period of 20 min by dividing the value transmitted to the tube of the plot (Rt_x), modified with its correction factor (Cf_x), by the value intercepted by the reference tube (Rt), and by subtracting the resulting value from 1:

$$Fi_x = 1 - ((Rt_x \times Cf_x) / Rt) \tag{1}$$

The amount of radiation intercepted by the plot x (Si_x) was calculated daily as the cumulative product of the fraction intercepted and the solar incident radiation calculated every 20 min:

$$Si_x = \Sigma(Fi_x \times I_0) \tag{2}$$

The cumulative amount of radiation intercepted by the plot was then the sum of the daily values.

5.4 Phenological measurements

Non-destructive measurements on five tagged plants in each plot were carried out from 7 DAT until flowering, on each day a net was installed or removed, at midway during each shading period and three to four days after the removal of each net. Production of fully expanded blades on the main tiller was recorded by noting leaf collar appearance until the flag leaf. A leaf was considered as fully expanded once its collar was visible above the enclosing sheath of the previous leaf. Values were recorded with decimals for better precision, +.5 when approximately half of the blade of the following leaf had already appeared. The mean of the number of collars was kept as the fully expanded leaf number corresponding to the day under study. The youngest leaves were tagged on the day of observation with rings of different colors with regards to their position in order to avoid errors at late stages due to leaf senescence and abundant foliar development. Total and green tiller number, sheath length (distance from the base of the plant up to the highest collar) and canopy height (distance from the base of the plant until the tip of the highest leaf) were measured systematically. Panicle initiation (PI) of the main tiller was observed under a binocular microscope (Leica MZ 9₅, Leica Microsystems Ltd., Heerbrugg, Switzerland) by dissecting plants collected in each plot every second day close to PI. Initiation was deemed to have occurred when the first row of floral primordial was visible on the shoot apex. Heading was defined as the time when 50% of the panicle has exserted from the flag leaf sheath. Anthesis was determined in each plot when an average of 50% of spikelets per panicle had exserted their anthers.

5.5 Destructive morphological measurements and calculations

Seedlings were sampled on the day of transplanting as 3 sets of 12 seedlings each. Quadrats were sampled in all the plots on each day a net was installed or removed, at midway during each shading period (this sampling concerns only Rad0 and the plots with net at the time of the sampling) and three to four days after the removal of each net. Sampling areas were 0.32 m^2 (40 x 80 cm, 8 hills) until PI and 0.08 m^2 (20 x 40 cm, 6 hills) after PI. Seven rows were left from the border of each treatment to avoid considering plants that were lighted at sunrise or sunset despite the presence of the net and to leave enough available area in Rad0 plot to establish each Iso treatment. For each sampling date, plants with most of their rooting system were collected early morning and placed in a plastic bag containing 5 to 6 cm of water. The plastics bags were placed in a cooler with ice and then brought to the air condionned lab for cleaning under running water and subsequent analysis. From each sampling, green and dead tillers were counted systematically from all plants, sheath length of half of the plants was measured as the distance from the base of the plant to the highest collar and green and dead leaf blades were detached from the green tillers on all plants. The area of the green blades of all plants until 21 DAT (mid-tillering), of a sub-sample of 4 or 3 randomised plants before and after PI, respectively, was measured with a leaf area meter (MK2, Delta-T Devices Ltd., Cambridge, UK) and the total stem length of the same plants was calculated as the sum of the stem length (from stem base to highest collar) of each individual stem. Sheaths, from 26 DAT onwards, and juvenile panicles, from 49 DAT onwards, were systematically detached from the stem of the remaining plants (those non analysed for leaf area) and juvenile panicles were counted. Green blades of the dead tillers were also separated from the stem. For all sampling dates, dry weight of each entities, green and dead leaf blades, leaf sheaths, internodes and panicles (when present) of each sub-sample of the green tillers, and also green and dead leaf blades and leaf sheaths of the dead tillers, was determined by weighting the material after drying during 48 h in the oven at 70 °C.

Stem dry weight was calculated as the sum of sheath and internodes dry weight. Specific stem length (SSL, cm g^{-1}) was calculated by dividing the total stem length by the corresponding stem dry weight. Specific leaf area (SLA, cm^2 g^{-1}) was calculated by dividing leaf blade area by the corresponding leaf blade dry weight. Total green leaf blade area (LA, cm^2) was determined from the product of total green leaf blade dry weight and SLA. The last three variables corresponded to the green tillers only. Leaf area index (LAI) was calculated as the total green leaf blade area of the plant, the sum of the green area of the green and dead tillers, divided by the corresponding sampling area. Total leaf blade dry weight was calculated as the sum of green and dead leaf blade dry weight. Shoot dry weight of the plants was calculated as the sum of the dry weight of leaf blades, stems and panicles. All measurements were determined on a per plant basis by dividing each variable by the number of plant per plot.. Partitioning coefficient of the dry matter was calculated between each sampling date by dividing the increase in dry weight of each individual organ (leaf blade, leaf sheath, internode and panicle) by the corresponding increase in shoot dry weight. For this purpose, leaf blade dry weight was considered as the sum of green and dead leaf blades and leaf blade and sheath dry weights were assumed stable as soon as their maximal value per plant was reached, i.e. no material loss was considered. Tagged plants were sampled 71 DAT for main tiller analysis only. Each main tiller, and its leaf blades and sheaths, was separated from the whole plant, and green leaf blade area, stem length, dry weight of green and dead leaf blades, leaf sheaths, internodes and panicles, and grain number per panicle were determined, as well as SLL and SLA calculated.

5.6 Validity of the results

Dynamics with days after transplanting of highest collar height and green tiller number per plant from non destructive and destructive measurements were compared in order to check if these data were consistent. Highest collar height of Rad0 was similar for both methods (Fig. 3a), whereas it appeared slightly higher for destructive measurements when considering Rad5 (Fig. 3b). Green tiller number per plant was similar between non destructive and destructive measurements for rad5, whereas it was appreciably higher for destructive when considering Rad0 (Fig. 3c). The lowest values observed for some non-destructive measurements can be attributed (i) to tagging, that might have disturbed the plant itself and the surrounding soil region because of regular manipulations, and (ii) to difficulties, because of continuous flooded water, to count the very young tillers or to identify the exact plant base to measure the length. For these reasons, highest collar height from the ground and green tiller number per plant in the subsequent analysis will be those obtained from destructive measurements.

6 - Results

6.1 Climatic measurements

Fraction of transmitted radiation was 1.0 in Rad0 at 10 days after transplanting (DAT) when the seedlings were still too small to be detected by the sensor (Fig. 4a). This fraction decreased down to 0.1 at 60 DAT. Fraction of transmitted radiation in Rad5 was 0.28 at 10 DAT, confirming that 70% of the incoming radiation was absorbed by the net (Fig. 4a). The fraction in Rad5 decreased down to 0.1 at 50 DAT and then increased up to 0.27 just at the time when the net was removed from the plot. Fraction of transmitted radiation in Rad1 was similar to that of Rad5 until 18 DAT, when the net was removed from the plot. The fraction was then as high as 0.9, higher than in Rad0 because the seedlings in Rad1 were smaller than those in Rad0 that did not experienced any reduction in incident radiation. Fraction in Rad1 was thereafter always higher than that in Rad0, confirming that the plants in Rad1 were smaller at least until 60 DAT. Fraction in Rad2 were similar than that in Rad0 until the net was set up 22 DAT (Fig. 4a). From that date, the fraction in Rad2 was lower than that in Rad5 since the plants in Rad2 were bigger. The fraction in Rad2 became similar to that in Rad1 and higher to that in Rad0 right after the net removal 30 DAT. Fraction measured in Rad3 and Rad4 were similar to that in Rad0 until the time when the net was set up at 35 and 44 DAT, respectively (Fig. 4b). The same fractions became higher than that in rad0 as soon as the net was removed from each plot.
Cumulative intercepted radiation in Rad0 was very close to 0 until 20 DAT, then increased up to 800 MJ m^{-2} at 65 DAT (Fig. 4c). The same dynamics as that for Rad0 applied to the cumulative intercepted radiation calculated in Rad1 and Rad2, but with a delay of about 4 days due to the previous presence of the net. The dynamics calculated in Rad5 departed strongly from the previous ones, as only 100 MJ m^{-2} was reported at 55 DAT, time when the values increased rapidly following the removal of the net, until 350 MJ m^{-2} reported at 65 DAT (Fig. 4c). The cumulative intercepted radiation calculated in Rad3 and Rad4 were similar to Rad0 until 35 and 44 DAT, respectively (Fig. 4d). Both dynamics were similar from 53 DAT when the net was removed from both treatments and the value at 65 DAT was 600 MJ m^{-2}. The cumulative incident radiation during the periods when the net was placed in Rad1 and Rad2 was lower by only 30 MJ m^{-2} than that calculated in Rad3 and Rad4, indicating that the impact of the treatments on incident radiation were close.

Daily maximum meristem temperature measured in Rad0 from 10 to 35 DAT (Fig. 5a), period when the meristem was at soil level, was higher than that of the air measured at 2 m height by 4 to 8 C most of the time. From 35 DAT, both temperatures were close. Daily minimum meristem temperature was higher than that of the air, by 1 to 4 C. Similarly, daily maximum meristem temperature measured in Rad0 was higher than that of Rad5 up to 6 C (Fig. 5b). Daily minimum meristem temperatures for both were close. The variability between meristem temperature and air temperature, and between meristem temperature in Rad0 and Rad5, imply the use of thermal time for data analysis. Hence, thermal time, with a base temperature of 12C, was calculated independently for each treatment.

6.2 Phenological plasticity to the reduction in light interception

Increase in main stem leaf number (MSB) with thermal time in Rad0, observed from non destructive measurements, can be described with 2 linear phases: a first one from transplanting until around 450 °C days, time corresponding to the emergence of the collar of leaf 12, and the second from 450 °C days until flag leaf 17 appearance 940 °C days after transplanting (Fig. 6a). In Rad1, Rad2 and

Rad5, increase in MSB was similar to that in Rad0 until 800 °C days, described with 2 linear phases with change in slope at around 450 °C days (Fig. 6a), although dynamics in Rad2 and in Rad5 were slightly delayed compared to that in Rad0. In Rad1, the final MSB was similar to that of Rad0, with a value of 17.4 blades observed at 940 °C days. In Rad2 and Rad5, the flag leaf appeared at around 850 and 800 °C days, respectively, with a respective total leaf number of 16.4 and 16.0. No difference was observed in the increase in MSB with thermal time between Rad3, Rad4 and Rad0 (Fig. 6b). Panicle initiation was observed at close dates among the treatments, at 560 °C days in Rad5, 580 in Rad2, 590 in Rad1 and 605 °C days in Rad0, Rad3 and Rad4 (data not shown). Flowering time did not appreciably vary among treatments. It occurred at 970 °C days in Rad5, 980 in Rad2, 990 in Rad3, 1000 in Rad0, 1015 in Rad4 and 1025 °C days in Rad1 (data not shown).

The same pattern with thermal time was observed in dynamics of highest collar height at plant level for Rad0 to Rad5 (Figs 6c and d): increase in height could also been described with 2 linear phases, a first one with a low slope until 750 °C days from 15 to 30 cm, and a second one with a high slope thereafter until a final height of 70 cm reached at 1000 °C days (Figs 6c and d). In Rad1, the values were lightly lower from 817 to 1025 °C days but the value of the maximum collar height did not differ significantly among Rad1 and Rad0 (69 cm for Rad1 against 71 cm for Rad0, Fig. 6c). In Rad5 however, the dynamics in collar height was strongly affected between 892 °C days and flowering (973 °C days) and the height of the highest collar at flowering was 60 cm (Fig. 6c).

Increase in canopy height in Rad0 was linear from transplanting until 700 °C days (Fig. 6e). A cessation was then noted between 700 and 780 °C days, when the increase in canopy height resumed linearly at a higher rate than during the first phase. A similar pattern in the increase in canopy height was observed in Rad1 and Rad2 (Fig. 6e), and in Rad3 and Rad4 (Fig. 6f). Canopy height at flowering was 85.4 cm in Rad1, 90.7 cm in Rad2, 85.5 cm in Rad3 and 81.2 cm in Rad4. Increase in canopy height in Rad5 was slightly ahead of the other treatments, but no cessation was visible between 700 and 780 °C days, when the slope of the increase was higher than before 700 °C days.(Fig. 6e). At 894 °C days, canopy height in Rad5 was 88.8 cm.

6.3 Dry matter partitioning in response to the reduction in light interception

Plant shoot dry weight (SDW) measured in Rad0 increased exponentially with thermal time throughout the plant development until 40 g per plant was measured at 1000 0C days (Fig. 7a). Dynamics in Rad1 and Rad2 were similar, but were delayed during the shading period establishment (Fig7a, inset). SDW in Rad0, Rad1 and Rad2 was 10.63 g at 562 °C days, 8.73 g at 551 °C days and 8.08 g at 551 °C days, respectively (Fig 7a). The values of the SDW were lower in Rad1 and Rad2 compare to Rad0 throughout plant growth. From 900 °C days, the SDW value in Rad0 increased slower than in Rad1 and Rad2. The final SDW was 41.3 g in Rad0, 47.4 g in Rad1 and 44 g in Rad2 at 1000, 1020 and 980 °C days respectively. Increase in plant shoot dry weight in Rad5 departed appreciably from that in Rad0, and even was null from 650 to 800 °C days (Fig. 7a). At 780 °C days at net removal, SDW was 6.7 g, and increased strongly after shading and was 23.7 g at flowering. Increase in Rad3 and Rad4 was strongly affected from the time the net was set up (Fig. 7b). SDW in Rad4 did not increase at all during the shading period, from 700 to 850 °C days, which corresponded to the same period when no increase of SDW was noted on Rad5. Increase in SDW in Iso4 was much quicker than that in Rad0 as a response of the thinning and SDW reached 56.4 g at 891 °C days (Fig. 7b). After shading, SDW in Rad3 and Rad4 reached a final value of 38.7 g and 32.1 g, respectively, similar to that in Rad1.

Variation in specific leaf area (SLA) and specific stem length (SSL) with thermal time were analysed from transplanting until flowering in all the treatments (Fig. 7c and d). SLA in Rad0 decreased right after transplanting, and probably as a response to the transplanting event, from 365 $cm^2\ g^{-1}$ down to 240 $cm^2\ g^{-1}$ at 130 °C days (Fig. 7c). It then increased back to 260 $cm^2\ g^{-1}$ at 220 °C days and remained fairly constant until 450 °C days. From that time, SLA decreased down to 210 $cm^2\ g^{-1}$ at 700 °C days, and then increased to 230 $cm^2\ g^{-1}$ at 770 °C days and remained constant until flowering. SSL measured in Rad0 decreased quickly from 260 cm g^{-1} to 140 cm g^{-1} between 280 and 310 °C days, and then more gradually to 40 cm g^{-1} at 800 °C days and then remained stable until flowering (Fig. 7e). SLA in Rad5 increased strongly compared to Rad0 as soon as the net was set up, and was measured at 300 $cm^2\ g^{-1}$ at 200 °C days. It remained always significantly higher than in Rad0 thereafter, down to 240 $cm^2\ g^{-1}$ at 980 °C days, with a transient reduction at the time when the net was removed (Fig. 7c). SSL of Rad5 was always significantly higher than that of Rad0 until 650 °C days, from which the values were quite close (Fig. 7e). SLA and SSL in Rad1 varied similarly as in Rad5 during the time when the net was on (Figs 7c and e), although the first measurement of SSL was a bit late to distinguish the effect. As soon as the net was removed, variation of SLA and SSL in Rad1 was similar as that in Rad0. SSL in Rad2 varied similarly as in Rad0 during the time the net was not on, and similarly as in Rad5 during the shading period (Fig. 7e). SLA in Rad2 was similar as that in Rad0 until the net was on, then it increased, not as high as in Rad5, up to 290 $cm^2\ g^{-1}$ at 450 °C days, time when the net was removed (Fig. 7c). SLA decreased continuously thereafter, but was never as low as in Rad0, except from 800 °C days. SLA and SSL in Rad3 increased as soon as the net was set up, up to 270 $cm^2\ g^{-1}$ and 80 $cm\ g^{-1}$ at 250 °C days, then decreased down to the values measured in Rad0 as soon as the net was removed from the plot (Figs 7d and f). Same remarks are valid for SLA and SSL in Rad4, except that the differences with Rad0 at the time when the net is on, were non significant (Figs 7 d and f). SLA in Iso4 was significantly lower by 10 $cm^2\ g^{-1}$ than that in Rad0 from the time the thinning was established (Fig. 7d), whereas SSL was not affected (Fig. 7f).

Green tiller number per plant in Rad0 increased rapidly with thermal time from 150 until 450 °C days, when tiller number was 27 (Fig. 7g). It increased then more slowly until 650 °C days, when the maximum tiller number was 31. From that time, green tiller number decreased down to 18 due to tiller senescence. Green tiller number in Rad1 almost remained constant at 5 during the shading period from 200 to 300 °C days (Fig. 7g). As soon as the net was removed, the slope of the increase in tiller number was similar to that in Rad0 until 450 °C days, when tiller number was 18. From 450 °C days, the slope was then lower but similar to that of Rad0 during the same period. Maximum tiller number per plant in Rad1, 27, was reached at 680 °C days. The increase in green tiller number in Rad2 was significantly reduced during the shading period. As soon as the net was removed at 450 °C days, the slope of the increase in tiller number was similar to that in Rad0 and that in Rad1 of the same period (Fig. 7g). The maximum tiller number and the time when it was reached was equivalent as those in Rad1. Tiller number at flowering in Rad1 and Rad2 were 22 and 25, respectively, higher than that in Rad0 due to a lower tiller senescence. Increase in tiller number in Rad5 was slow from 4 at 210 °C days to 11 at 900 °C days, time when the net was removed and the increase in tiller number increased rapidly (Fig. 7g). Green tiller number per plant in Rad3 decreased quicker than that in Rad0 from the time the net was placed above the crop (Fig. 7h), but no significant difference was then observed from 750 °C days. Green tiller number in Rad4 was not significantly different from that in Rad0. Green tiller number in Iso4 increased after a delay of 100 °C days after thinning at a similar rate than that observed during the first phase in Rad0 (Fig. 7h). Tiller number was 33 at 820 °C days. The productive tiller number per plant at flowering was significantly higher in Rad2, Rad3 and Rad4, between 16 and 18, than that in Rad0, 14 (Fig. 7h inset). The value reported in Rad5, 10, was the lowest.

Dynamics in leaf area index (LAI) with thermal time was a consequence of dynamics in green tiller number per plant (Fig. 7i). LAI increased rapidly from 300 until 800 °C days in Rad0 up to a maximum of 6 (considering a strange value at 650 °C days). The dynamics of LAI in Rad1, Rad2 (Fig. 7i) and Rad3 (Fig. 7j) was affected from the time the crop was shaded but the rate in LAI increase was thereafter similar to that in Rad0. at 900 °C days, the same maximum value was measured for these situations. Dynamics in LAI for Rad4 was not significantly different from that of Rad0 (Fig. 7j). Dynamics in LAI for Rad5 was slow until 800 °C days, when LAI was 2, and then resumed to the same rate as in Rad0 after the net removal (Fig. 7i). The LAI measured in Iso4 was obviously close to half of that measured in Rad0 just after thinning, but then it increased at a similar rate as that in Rad0 and the value at 900 °C days was 4 (Fig. 7j).

Change with thermal time in the dry weight and partitioning coefficient of each above-ground organ, green and dead leaf blades, leaf sheaths, internodes and panicles was analysed on Fig. 8. Internode elongation started at 450 °C days, just at the time when a break in slope of the increase in main tiller leaf number and green tiller number per plant was observed (Figs 6a and b and Figs 7g and h). From transplanting until the onset of internode elongation (600 °C days), partitioned coefficient of leaf sheath and green leaf blades were 55 and 45 % of the shoot dry weight, respectively (Fig. 8b). Rapid start in internode elongation, was noted at 600 °C days, at the same time as PI was observed and tiller emergence stopped (Fig. 7g and h). Internode dry weight increased rapidly from 600 to 972 °C days to reach 11.3 g at flowering (Fig. 8a) and a partitioning coefficient of 0.7 at 800 °C days (Fig. 8b). Panicle dry weight per plant increased rapidly from 750 °C days, just at the time when a rapid increase in collar and canopy height (Figs 6c, d, e and f), as well as a transient increase in SLA (Figs 7c and d), were observed. Panicle dry weight reached the value of 6.4 g at 1004 °C days (Fig. 8a). Partitioning coefficient to the panicle was the highest at 915 °C days, 0.8 (Fig 8b). At that time, the partitioning coefficient of internode was only 0.2, but, at 972 °C days, the partitioning coefficient of internodes and panicles reversed and the partitioning coefficient for internodes was 0.63. This change could be explained by the priority given to internode growth for panicle exsertion.

The increase in dry weight of green leaf blades, leaf sheaths, internodes, panicles and dead leaf blades was analysed with thermal time for all the treatments on Fig. 9. Shading periods imposed at distinct vegetative growth stage affected the dry weight dynamics of all the organs of the plant. In Rad0, green leaf blade (LDW) and leaf sheath dry weight (SeDW) increased lightly from transplanting to 560 °C days after emergence (Figs 9a and c). After 560 °C days, SeDW increased rapidly up to 16.6 g and then decreased to 13.4 g at flowering due to senescence of the tillers (Fig. 9c). LDW increased up to 700 °C days and then tended to remain constant at 10 g (Fig. 9a). Internodes and dead leaf blade dry weights (IDW, dLDW) increased strongly from 630 °C days, time that corresponds to start in internode elongation and tiller senescence (Fig. 7g). At 1000 °C days, IDW, panicle dry weights (PDW) and dLDW were 11.26, 6.4 and 1.2 g in Rad0 (Figs 9e, g and j). Organ dry weights differed greatly among treatments, but relative differences among organs within the treatment were similar in Rad1 and Rad2 for the LDW, SeDW, IDW and PDW to that found in Rad0 (Figs 9a and c). Dry weight was affected significantly at the beginning of the shading treatments for LDW and SeDW, and then tended to follow the same pattern as that in Rad0. Organs dry weights were lower than those in Rad0 throughout plant growth except at flowering when it was higher. A similar pattern was observed for the shoot dry weight (Fig. 7a). LDW, SeDW, IDW and PDW at flowering were 10.1, 15.5, 13.2 and 7.5 g in Rad1 and 10.4, 14.3, 11.2 and 7.5 g in Rad2. LDW and SeDW in Rad3 were mainly affected during shading. Dry weight of these organs was significantly reduced. Increase in LDW in Rad3 resumed that in Rad0 from 760 to 990 °C days and was relatively constant during this whole period. In contrast to the variation in LDW, SeDW in Rad3 was always lower than that in Rad0 until flowering (Fig. 9d). Increase in IDW and PDW in Rad3 was similar to that in Rad0 (Fig. 9 f and h). LDW, SeDW, IDW and PDW in Rad3 at flowering were 9.2, 11.5, 10.9 and 5.6 g. If LDW in Rad4 was not affected by shading (Fig. 9b), increase in SeDW, IDW and PDW in Rad4 were strongly affected or even stopped (Figs 7d, f and h). As soon s the net was removed from the crop in Rad4, biomass accumulation increased strongly in the plant until flowering to reach the same value for SeDW (13.3 g) and IDW (11.8 g) than that in Rad0. PDW, 5.1 g at 1000 °C days, was lower than in Rad0 mostly because increase in SeDW and IDW were highly delayed. Shading from 130 to 780 °C days in Rad5 has strongly affected biomass accumulation. Increase in LDW, SeDW and IDW was slow during the whole period and respective values at 780 °C days were 3.2, 2.7 and 0.7 g. As soon as the net was removed, dry matter accumulation for each organ increased rapidly and dry weights at flowering for LDW, SeDW and IDW were 6.3, 7.6 and 6.0 g respectively (Figs 9a, c and e). Rapid increase in organ dry weight was measured in Iso4 as soon as the plot was thinned, from 30 % for LDW, SeDW and IDW (Figs 9b, d and f) and 40 % for PDW (Fig. 9h). At 900°C days, dry weights of LDW, SeDW, IDW and PDW were 15.4, 28.0, 11.9 and 4.4 g respectively. Variation in dLDW was not significantly different among the treatments (Figs 9i and j), except for Rad5 where dead leaf blades dry weight was close to zero (Fig. 9 i).

The dynamics of the partitioning coefficients (PC) of each organ with thermal time (Fig. 10) were obtained from the variation in organ dry weight presented on Fig. 9. Shading periods for all treatments induced an increase in the PC for leaf blade (PcLB) to the detriment of leaf sheaths (PcLS): dry matter accumulation in the leaf blade was higher than that in the leaf sheath compared to that in Rad0 (Figs 10a and b). After the shading periods, an increase in PcLS together with a decrease in PcLB induced the values to be similar to those in Rad0. Partitioning coefficient for internodes (PcI) and partitioning coefficient for panicles (PcP) increased when those for blades and sheaths decreased (Figs 10c and d). Dry matter in internodes was accumulated first in Rad0, regarding values of PcLB and PcLS (Fig. 10c). As the decrease in partitioning coefficient for leaf blades and leaf sheaths was delayed in Rad2, PcI was then highly delayed. PcP were similar in all the treatments, except in Rad4 where this was lower, because partitioning to the internodes was the priority for those plants (Figs 10c and d). Despite this difference, PcI accounted for 60 % of the shoot dry weight per plant at flowering, and PcP for 40 % in Rad0, Rad2, Rad4 and Rad5. PcI and PcP accounted for 50% in Rad1 and Rad4.

SDW, PDW, total grain number (TGN), SLA and SSL of the main tiller of the tag plants were sampled 71 DAT (five days after the latest flowering, Rad1) and compared to check in what extent the treatments could have affected main tiller growth or if the main tiller characteristics were the same in all treatments. The values measured for Rad0 and Rad4 were not different, namely SDW were 3.2 and 3.3 g, TGN, 109 and 96, SLA, 188 and 186 cm^2 g^{-1} and SSL 43 and 42 cm g^{-1} in Rad0 and Rad4 respectively (Figs11a to e). In contrast, SDW and TGN measured in Rad1 were significantly higher compared to those of the control (Figs 11a to c). Values of SLA and SSL, 176 cm^2 g^{-1} and 28 cm g^{-1} respectively, were surprisingly and significantly lower and this was the reason for high SDW and TGN (Figs D and e). The tiller had to generate a big sink (TGN) to efficiently remobilise all the stored carbohydrates to the grain. The high PDW (1.1 g) measured in Rad2 is explained by the relative shorter crop cycle in this situation and the advanced accumulation of dry weight in the panicle (Fig. 11b). SLA and SSL were higher than those in Rad1 because part of the stored carbohydrates has already moved to the panicle. The same pattern than that in Rad1 is observed in Rad3 (relatively low SLA) but in a smaller extent (Fig. 11d). SLA in Rad5 is significantly high (Fig. 11d) since the growth conditions of this plot generated this crop to maintain a high SLA (Fig. 6c) during the whole crop cycle, even after the removal of the net. In contrast, SSL was low (Fig. 11e) since it was the organ that stored most of the assimilate gained by the plant in response to the low tiller density. As in the case of Rad2, PDW was significantly high since the crop cycle was shorter and the growth of the panicle started earlier (Fig. 11b).

Discussion

Shading of rice plants in the field by 70% during 9 consecutive days at distinct growth stages between early tillering and heading did systematically affect plant dry matter accumulation. The impact of shading on plant shoot dry matter was here similar in Rad1 and Rad2, and in Rad3 and Rad4, as both cumulative intercepted radiation and increase in dry matter after net removal were similar in Rad1 and Rad2, and in Rad3 and Rad4. The plant shoot dry matter, however, did not increase when the shading was applied during rapid internode elongation (Rad4 and Rad5), even if the morphological status of those plants at time when rapid internode elongation began was significantly different and if the cumulative total incident radiation was higher during that period than during the previous shading periods. This supports the general observation that low irradiance at any stage after panicle initiation is associated with lower grain yields (Pepper and Prine, 1972; Evans and de Datta, 1979). The time of rapid internode elongation is also the time when the loss by respiration is the highest in the plant (Saitoh *et al.*, 1998). Both growth respiration, due to the simultaneous growth of leaf blades, sheaths, internodes and panicles, and maintenance respiration, due to the presence of more mature organs, are increasing. Respiration at that stage competes then highly with the increase in shoot dry matter. Increase in shoot dry matter after the net removal resumed to a similar rate as that of the control plot, as it was also observed after a shading period at early grain filling (Kobata *et al.*, 2000). These authors reported also that the dry matter increase lasted appreciably longer than that in the control plot, thereby reducing the impact of the shading. This seems to be also the case in this study, even if tiller senescence affected the control plot more than the shaded ones.

Crop phenology (panicle initiation, flowering, maturity) was not appreciably affected by the shading even if the shaded period lasted from early tillering until shortly before heading (Rad5). Panicle initiation occurred just a little bit earlier in Rad2 and Rad5, probably because plants were shaded during the period preceding panicle initiation, but this was not visible anymore when flowering and maturity time were observed. Dynamics in leaf emergence of the main tiller was also remarkably stable under all these conditions, as it is commonly observed under variable climate conditions as long as it is thermal time driven and meristem temperature based (Stone *et al*., 1999; Lafarge and Tardieu, 2002). These observations support the statement that the increase in leaf number on the main tiller could be used as a time clock to model plant development (Gao *et al*., 1992; Nemoto *et al*., 1995). The succession of two linear phases to describe the dynamics in leaf emergence was also repeatable in this range of conditions. In the mean time, start in internode elongation, that was not affected by contrasted incoming radiation imposed at early stage and was then simultaneous for Rad0, Rad1 and Rad2, occurred at around 450 °C days. As a consequence, from 450 °C days, either leaf emergence rate and internode elongation competed for available carbohydrates, therefore reducing the amount of carbohydrates devoted to leaf elongation, or a change in plant structure would have increased the whorl length and thus the distance a leaf has to cover before its collar may appear. In the same way, the height of the main tiller (at highest tip or collar level) was not affected by the changes in growing conditions. The change in slope of the dynamics in plant height, however, was simultaneous with the start in rapid panicle growth, that could be a signal to change the plant strategy for assimilate partitioning. At the same time, an increase in SLA was observed probably to remobilize carbohydrates to the panicle or the sheaths. The results of this study, however, did not consider if the dynamics in leaf emergence of the branch tillers was affected by shading, but the dynamics in leaf emergence in rice has already been reported to be synchronous for all tillers of the plant in favorable conditions (Nemoto *et al*., 1995; Jaffuel and Dauzat, 2005). On sorghum, it was observed that dynamics in leaf emergence on all branch tillers was either maintained stable or fully stopped in response to high plant competition (Lafarge *et al*., 2002), but was never delayed. If this would also be the case for rice, the dynamics in leaf emergence would be a good parameter to estimate the crop demand for assimilate and the number of tillers that would stop their development, knowing that they are always the youngest ones (Lafarge, unpublished data).

Tiller emergence was significantly and rapidly affected by shading and full light exposure when these changes in growing conditions were imposed before maximum tillering. Tiller emergence was also able to resume 150 °C days after maximum tillering when the crop was thinned to half its initial density, even if tiller senescence had started already (Iso4). Emergence, however, resumed around 100 °C days after thinning in Iso4, whereas it resumed just after net removal in Rad1 and Rad2. Even if the plant is potentially able to produce tillers at any age, its time required to react to changes in growing conditions appears almost null before maximum tillering, but close to 100 °C days after it. During this delay, and before tiller emergence started again, the extra carbohydrates gained by the plant in Iso4 were stored in the leaf sheaths, while dry matter of leaf blades and internodes at plant level were similar to that of the control. This explains while SLA of plants from Iso4 was only slightly reduced when compared to that of control plants. As soon as new tillers emerged, dry matter of leaf blades, sheaths and internodes exceeded that of the control plants. Two consecutive phases describing tiller emergence with thermal time were observed: the first one lasted until 450 °C days and was characterized by a high slope (Rad0 and Rad1 after net removal) whereas the second one, from 450 °C days until maximum tillering, was characterized by a lower slope (Rad0, Rad1 and Rad2 after net removal). It is remarkable to note that the slope of each phase was observed on plants at the same growth stage but in contrasted canopies. Interestingly, the slope of tiller emergence in Iso4 observed after thinning was similar to the one of the first phase. This slope corresponds possibly to the potential tiller emergence rate of this variety, as this was stable in a large range in conditions. As for leaf emergence, start in internode elongation occurred at the time when the break in slope was observed on tiller emergence. As a consequence, from 450 °C days, tillering and internode elongation may compete for available carbohydrates, therefore reducing the slope of tiller emergence. Cessation in tiller emergence was simultaneous in Rad1 and Rad2 and occurred when LAI was close to 4 in both cases. In Rad0, the cessation was observed earlier, but also at a LAI close to 4 (as long as the strange LAI value observed in Rad0 just after 600 °C days was not considered). This common value of critical LAI close to 4, for which tiller emergence was observed to stop, is consistent with the range 3.4 to 4.1 reported by Zhong *et al*. (2002). Cessation in tiller emergence occurred also at the same time as panicle initiation was observed and rapid internode elongation began. Cessation in tiller emergence could then be controlled by the trophic status of the plant as a response of competition for carbohydrates due to internode elongation or by an internal regulation due to the high LAI or occurrence of PI and change in the plant strategy. The delay in tiller emergence reported in Rad1 and Rad2 induced a lower maximum tiller number per plant and delayed and reduced tiller senescence inside the crop. It even generated a higher tiller density at flowering in comparison with the control plots. As a result of the reduction in tiller emergence, dry matter dynamics at plant level of leaf blades, sheaths and internodes was similarly and significantly affected by early shading in Rad1 and Rad2 compared to that of control plants. In contrast, dry matter dynamics of the panicle in Rad2 was not affected mostly as a consequence of its shorter crop cycle. Even shading imposed shortly after panicle initiation affected slightly tillering by accelerating tiller senescence, but the impact was, however, higher on blade and sheath dry matter dynamics of the developing tillers. Shading during the rapid internode elongation affected strongly sheath and internode dry matter dynamics, whereas dry matter of leaf blades remained almost not changed as all the blades were likely to be already fully elongated at that time. Temporary cessation in the development of part of the tillers, most likely the youngest ones, was the most probable consequence of the shortage of assimilate in Rad3 and Rad4.

Increase in specific leaf area (SLA) and specific stem length (SSL) was observed just after the decrease in incoming radiation imposed by shading. Tardieu *et al*. (1999) also reported the high sensitivity of SLA to growing conditions and Lee and Heuvelink (2003) related the variability in SLA to the inverse of the daily incident radiation. The plasticity of SLA and SSL was reported at any plant stage considered in this study, from early tillering until rapid internode elongation, even if their range in variation decreased with plant stage according to the cessation in leaf emergence. Interestingly, the value observed in Rad5 after 300 °C days of shading was similar to that measured at early shading, probably indicating that the values observed in these conditions were the upper limit these variables could reach. This probable upper limit decreased with plant age as this was also observed for the value measured under normal conditions. Right after net removal, SLA and SSL decreased down to the same values as those measured on the control plants, immediately if before mid-tillering, but for a longer time if close to maximum tillering probably because of the higher competition for assimilate due to lower source/sink ratio. This supports the statement of Tardieu *et al*. (1999) that SLA cannot be used as a parameter to predict leaf area growth but is rather a consequence of leaf blade elongation and environmental conditions. These authors reported that SLA decreased when environmental conditions had a greater depressive effect on elongation rate than on photosynthesis and increased for the converse. The plasticity in SLA was also visible when change in partitioning occurred in the plant, as shortly after transplanting and at the start in internode elongation. Specific leaf area is defined by two components of the leaf blade, the leaf thickness and the leaf dry matter content, also known as the tissue density. The latter is considered as a good indicator of position on the resource use axis (Wilson *et al*., 1999). It is supposed here that leaf dry matter content, rather than leaf thickness that was relatively stable, was the component to have been affected by shading through the mobilization of soluble carbohydrates from the blade to other plant parts. Compensatory mobilization of reserves, as it was observed in this study, was also quantified in case of transient water drainage during grain filling in rice (Dingkuhn and Le Gal, 1996). In this situation, reserves mobilization had even increased grain yield by increasing the partitioning efficiency of assimilate (Yang *et al*., 2002) through hormonal changes (Yang *et al*., 2001). Specific leaf area at early stage is commonly used as an indicator to compare the vegetative growth strategy of plants that either colonize rapidly the available space and resources or invest in reserves and mechanical resistance (Peng *et al*., 1999). This strategy is dependent on the growing conditions in which the plants were bred (Poorter and De Jong, 1999). High specific leaf area at early stage is then a good factor to select plants for high competitiveness against weeds (Asch *et al*., 1999; Dingkuhn *et al*., 1999). The plasticity of SLA reported in this study highlights that, despite being a highly productive genotype, IR64 is still investing in reserves at early stage while colonizing space and has then the potential to be more efficient regarding weed competition.

The plasticity in SLA and SSL was also observed at tiller level few days after flowering. Low SLA and SSL were measured on main tillers of plants that experienced shading at early tillering stage (Rad1) and in a lower extent at the start in internode elongation (Rad3), whereas SLA and SSL calculated at the plant level did not show any significant difference with the control plants. It looks as if these plants were ready to face an extra period of shading by storing soluble carbohydrates at the main tiller level, like plants that experienced an early water stress did store carbohydrates in case a new stress would have occurred. In this study, however, this after-effect, as a consequence of the change in assimilate partitioning strategy in favor to the main tiller, was still visible around 6 weeks after the net removal. As a result, the sink size of this tiller, defined here by the grain number per panicle, increased most probably to meet the high availability of its reserves.

The partitioning coefficients (PC) to shoot organs were also affected in favor to leaf blade and to the detriment of leaf sheath whenever the shading occurred. This was significantly observed even during early internode elongation (Rad3 and Rad5) and was not affected by nitrogen status (Dingkuhn, 1996) since leaf nitrogen content was maintained at an optimal value through the plant cycle. Higher partitioning coefficient to leaf blade was also observed for cultivars with high weed competitiveness (Asch *et al*., 1999). Appreciable change in PC occurred during the transition from heterotrophic to autotrophic growth, but this was not considered in this study that started 15 days after transplanting. The partitioning coefficient to internode did change in all treatments because of the delay in plant development. No effect was observed on the partitioning coefficient to the panicle in this study since the nets were removed before heading, but shading during the early phase of grain filling was reported to increase the partitioning towards the panicle, and even towards the upper grain of the panicle (Okawa *et al*., 2003). Shading experienced by the crop in this study affected the partitioning coefficient to internode which may likely have a detrimental impact on grain yield as high partitioning coefficient to the stem close to flowering is a good way for achieving high yield (Samonte *et al*., 2001).

Conclusions and perspectives

Crop phenology and plant height of the rice plant were not affected by a 70% decrease in incoming radiation imposed at distinct plant ages between early tillering and mid-internode elongation. The phenology of the main tiller could then be used as the time clock of the plant development. The pattern of tillering was stable under full incoming radiation for contrasted canopies and dynamics in tiller emergence, and leaf emergence as well, could be divided into two main phases of distinct slopes until cessation in tiller emergence that would occur at a critical and stable value of LAI. The change in slope of leaf and tiller emergence would occur at the start in internode elongation of the main tiller. A framework of development relating the duration of elongation of all leaf blades, sheaths and internodes of all tillers of the plant to the internal time clock of the plant would then be required to simulate the plant leaf area growth. This kind of framework has already been developed on the main tiller of sorghum plants, with strong stability in contrasted growing conditions (Lafarge and Tardieu, 2002; Lafarge, unpublished data). On the basis of this framework, elongation of each organ of the plant would be simulated according to the time clock and thermal conditions and specific leaf area of individual leaves would be the consequence of the assimilate partitioning. The change in the partitioning coefficients with plant age is quantified already but the stability of the coefficients under different climate conditions should be checked. In case of the occurrence of a low incoming radiation period, then partitioning coefficients would be modified in favour to blades and carbohydrates would be mobilized from leaf blades and sheaths immediately. These modifications would be driven according to the potential range in variation of these two variables with plant age and an index of apparent competition for assimilate (Dusserre *et al*., 2002) as a result of the source:demand ratio, that has been successfully used to simulate tiller senescence (Lafarge and Hammer, 2002). Beyond these changes, tiller dynamics and organ dry matter would be affected according to the availability of the carbohydrates. The after-effect observed on the main tillers of early shaded plants, however, would need to be analysed more carefully.

Abstract

A field study was conducted at the International Rice Research Institute (IRRI), Philippines during the dry season of 2005 to quantify the impact on low light intensity on rice plant establishment. Shading was applied at 4 distinct vegetative growth stages, using a net that transmitted 30 % of light, without altering spectral composition. The objectives of this study were to quantify the variation in plant phenology, tiller dynamics, organ morphology and dry matter partitioning between the different organs. The priority between the competitive sinks of the plant and the main components responsible for the phenotypical plasticity of the plant were also evaluated and quantified in response to low incoming radiation periods for the 5 shading treatments compare to a control without shading. Non destructive measurement carried out to determine the main stem length, the collar and the canopy height revealed that crop phenology and plant height of the rice plant were not affected by a 70% decrease in incoming radiation imposed at distinct plant ages between early tillering and mid-internode elongation. The destructives measurements realised to quantify biomass partitioning in the different organs showed that assimilate partitioning was highly dependent on growing condition In case of the occurrence of a low incoming radiation period, then partitioning coefficients would be modified in favour to blades, and carbohydrates would be mobilized from leaf blades and sheaths immediately according to availability.

Résumé

Une expérimentation en champs fut conduite à l'Institue International de Recherche sur le Riz (IRRI), Philippines au cours de la saison sèche 2005 afin de quantifier l'impact d'un faible rayonnement sur la mise en place d'une culture de riz. Des ombrages ont été effectués à 4 périodes différentes du cycle végétatif de la culture. Pour cela, les filets noirs, diminuant le rayonnement de 70 % ont été placés à 30 cm au dessus de la canopée; il été montré au préalable que les filets n'altéraient pas la composition spectrale de la lumière. Les objectifs de cette expérience étaient dans un premier temps de voir l'effet de ces ombrages sur la phénologie de la plante, le dynamique de tallage, la morphologie des organes et la réparation de la matière sèche entre ces derniers; et, dans un second temps de caractériser la plasticité du taux de répartition de la matière sèche, tout en identifiant les puits prioritaires pour l'accès au ressources carbonées lorsque les conditions de rayonnement sont limitantes et non limitantes. Les résultats des mesures non destructives ont permis de mettre en évidence que la phénologie de la plante (le nombre de feuilles de la tige principale, la hauteur de la gaine et de la canopée) n'est pas affectées lorsque le rayonnement est fortement diminué du début du tallage jusqu'à mi-élongation des entre-nœuds. Parallèlement, les mesures destructives réalisées, afin de quantifier la répartition de la biomasse entre les différents organes, ont mis en évidence que la répartition des assimilats au sein de la plante était fortement dépendante des conditions de culture. Lorsque le rayonnement est faible, le coefficient de répartition de la matière sèche est modifié en faveur de la feuille, et les carbohydrates seraient remobilisés immédiatement, des feuilles et gaines vers d'autres organes puits, en fonction de leur disponibilité.

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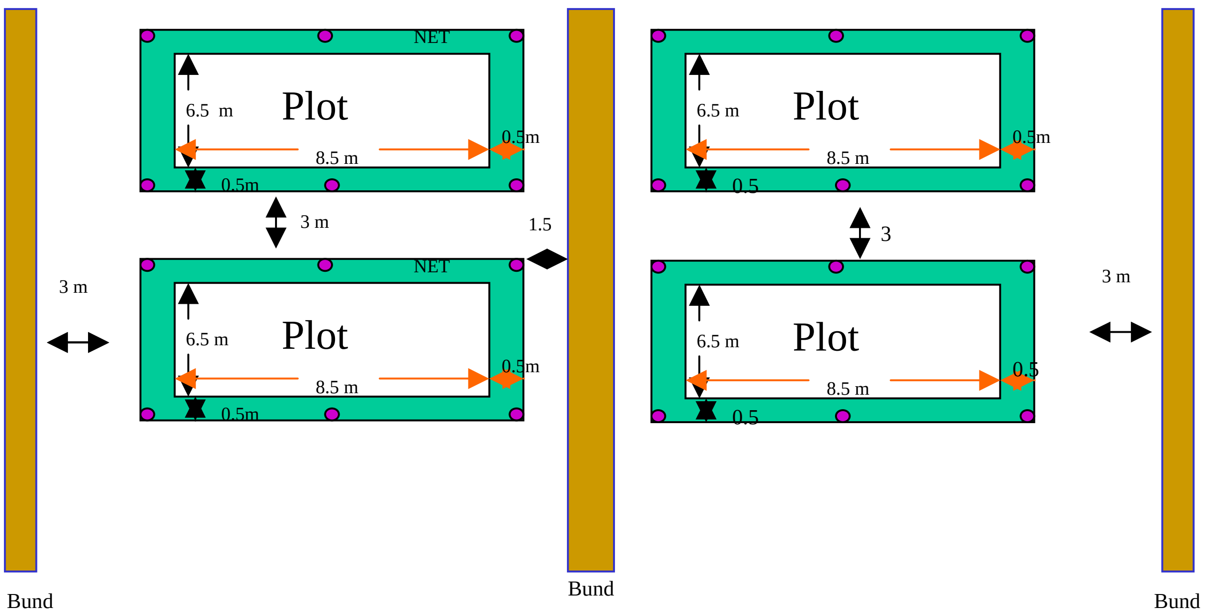
Annexes

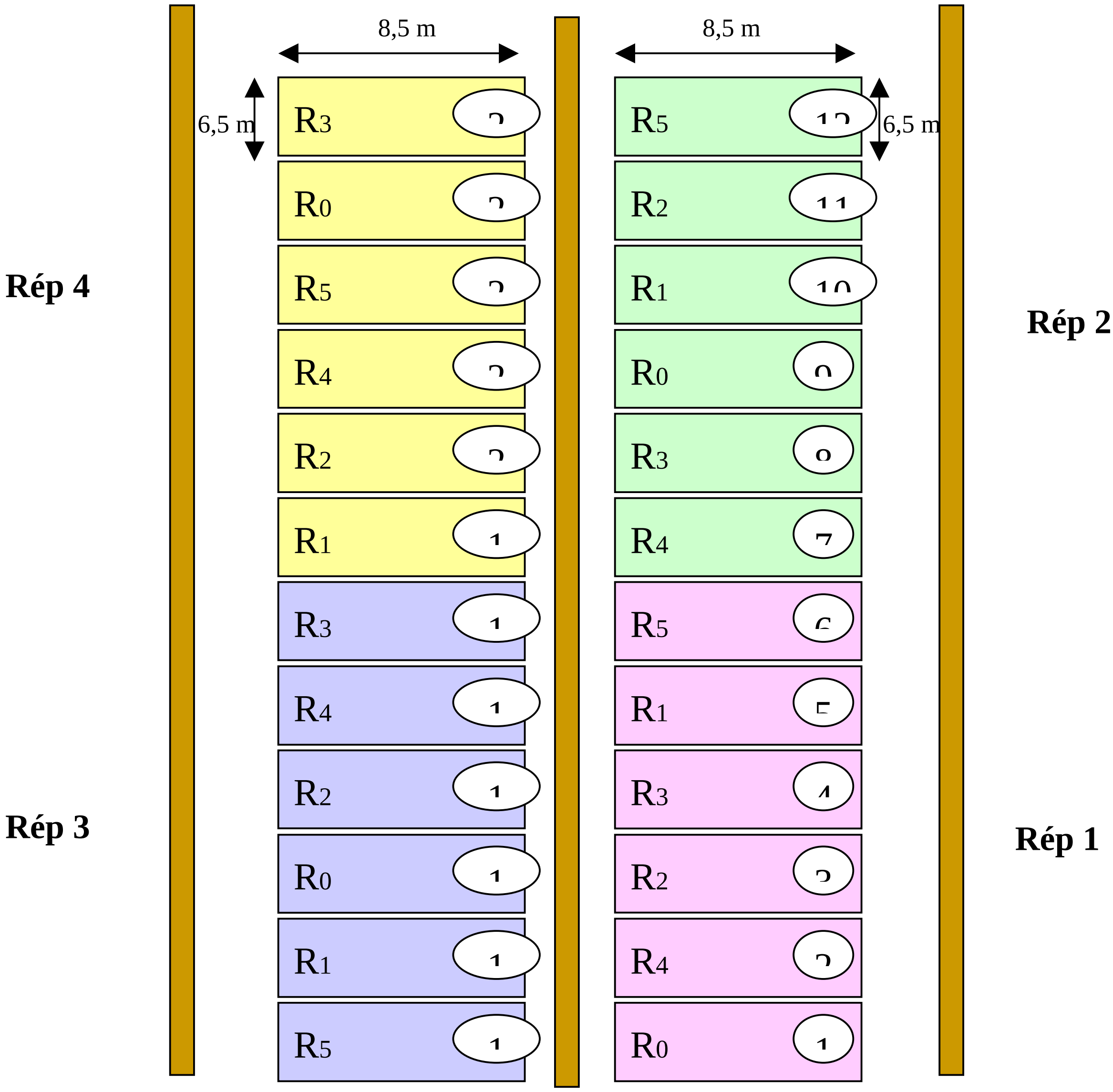
Annexe 1 - Rice paddy production in 2003 for the 10 most important rice producers (source FAO).

Top 10 rice producers, 2003 (paddy production in metric tons)	
1. China	166,000,000
2. India	133,513,000
3. Indonesia	51,849,200
4. Bangladesh	38,060,000
5. Viet Nam	34,605,400
6. Thailand	27,000,000
7. Myanmar	21,900,000
8. Philippines	13,171,087
9. Brazil	10,219,300
10. Japan	9,863,000

Annex 2 – Plot design



Annex 3 – Layout of the experimentation



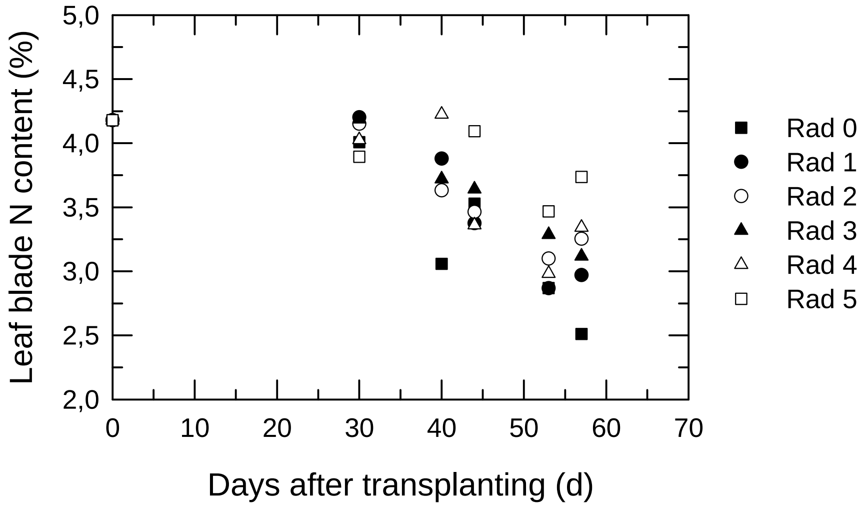
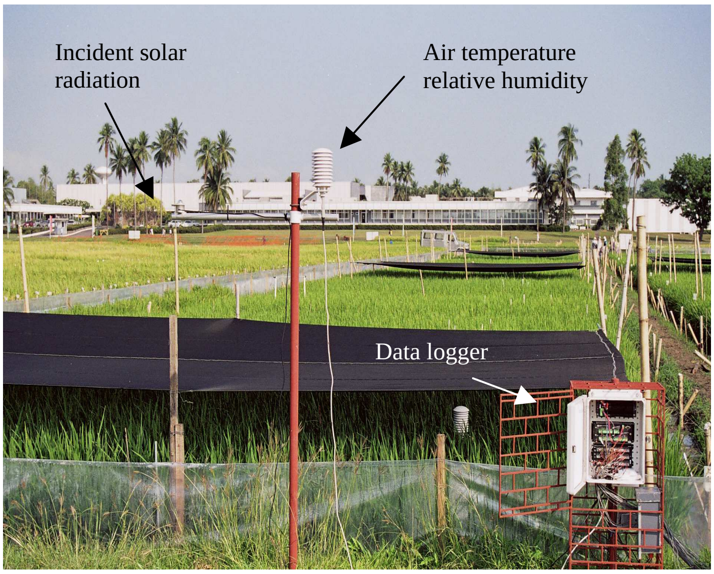


Fig. 1. Changes with DAT (days after transplanting) from transplanting in leaf blade N content per plant for Rad0 (■), Rad1 (●), Rad2 (○), Rad3 (▲), Rad4 (Δ) and Rad5 (□).



Incident solar radiation, air temperature and relative humidity measurements collected in the data logger.

Solarimeter above the ground level diagonally across three rows

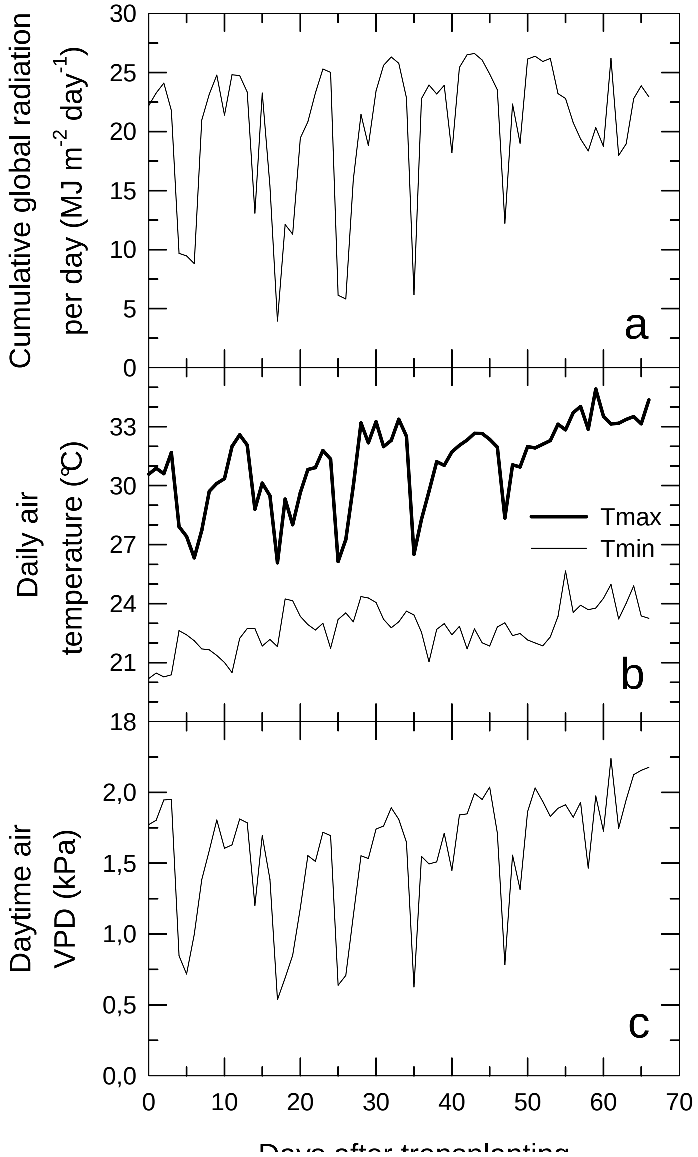


Fig. 2. Changes with DAT in cumulative global radiation per day (a), daily temperature (b) and air vapour pressure deficit (VPDa) (c). Data were average with a daily time step.

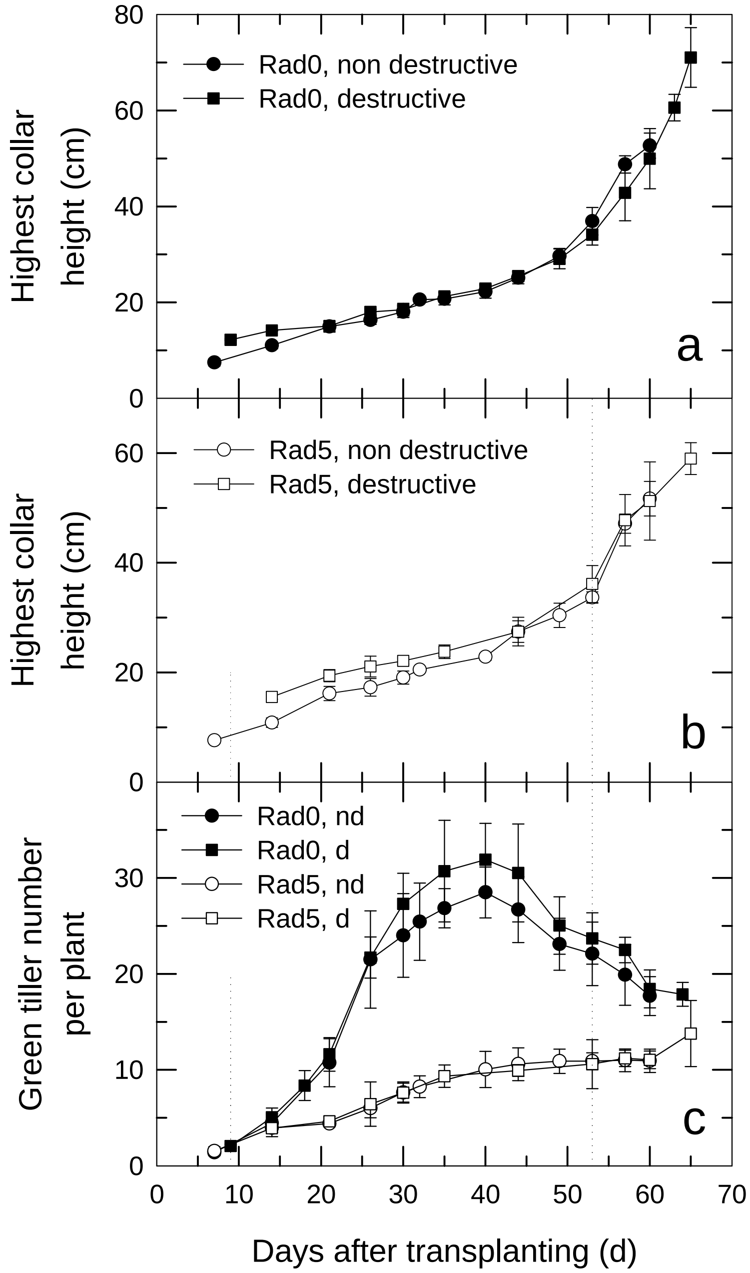


Fig. 3. Changes with TT from transplanting to flowering in highest collar height (a-b) and green tiller number (c) in non-destructive measurement for Rad0 (●) and Rad5 (○), and destructive measurement for Rad0 (■) and Rad5 (□). Timing of shading treatment in Rad5 is indicated by interval in dotted.

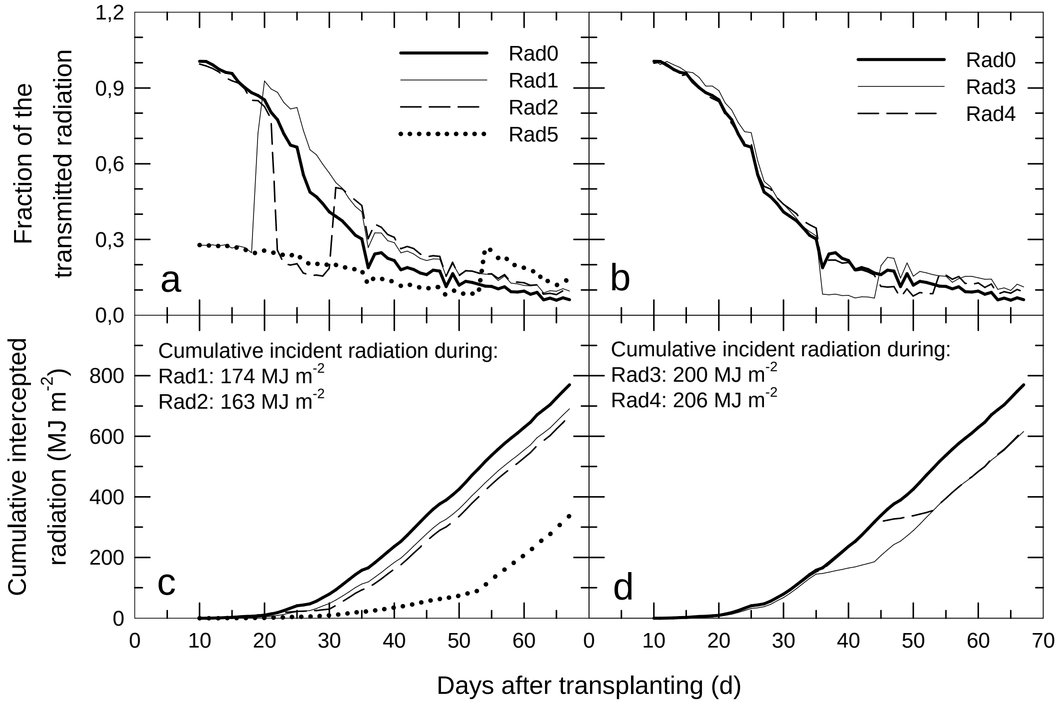


Fig. 4. Changes with TT in fraction of transmitted radiation (a-b) and cumulative intercepted radiation (c-d) for Rad0 (thick line), Rad1 and Rad3 (thin line), Rad2 and Rad4 (dashed line), and Rad5 (dotted line).

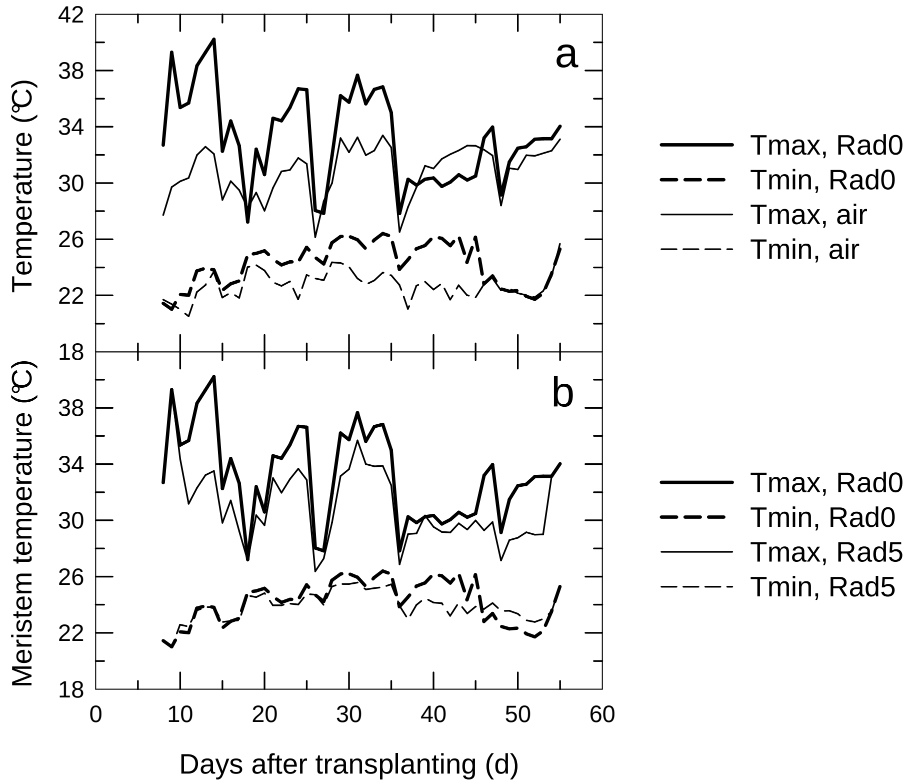


Fig. 5. Changes with DAT in air temperature (a) (Tmin: thin dashed line and Tmax: thin line) and meristem temperature (a-b) in Rad0 (Tmin: thick dashed line and Tmax: thick line) and Rad5 (Tmin: thin dashed line and Tmax: thin line). Meristem temperature was assumed to correspond to soil temperature (Ts) until start in internodes elongation (time when plant meristem was above water level) and to canopy temperature at meristem height until heading (Tci) and at panicle height thereafter (Tco).

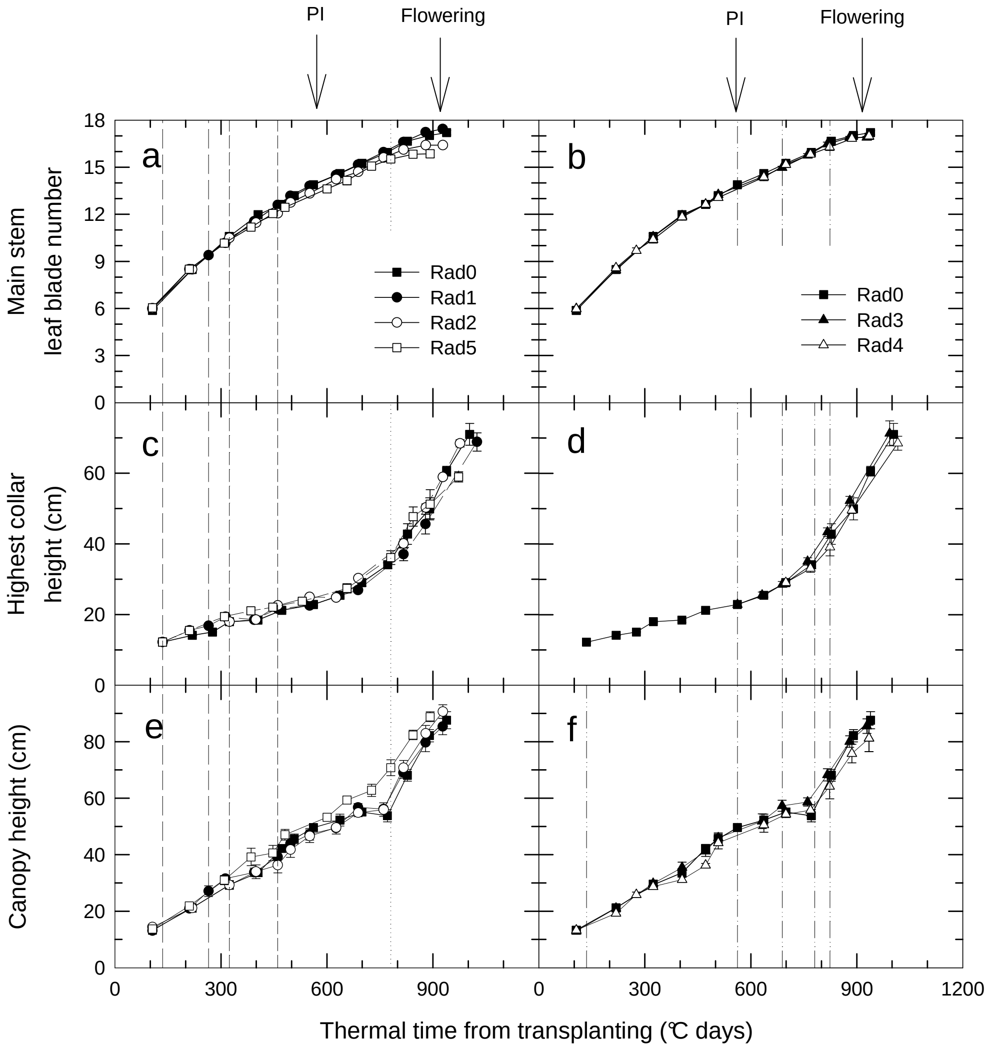


Fig. 6. Changes with TT in main stem leaf blade number (a-b) and canopy height (e-f) for the non-destructive measurements, and highest collar height (c-d) for the destructive measurements. Timing of shading treatment is indicated by interval in med-dash lines for Rad1, short-dash lines for Rad2, dash-dot lines for Rad3, dash-dot-dot lines for Rad4 and dotted lines for Rad5. Verticals lines represent the standard error of the mean of the four replications.

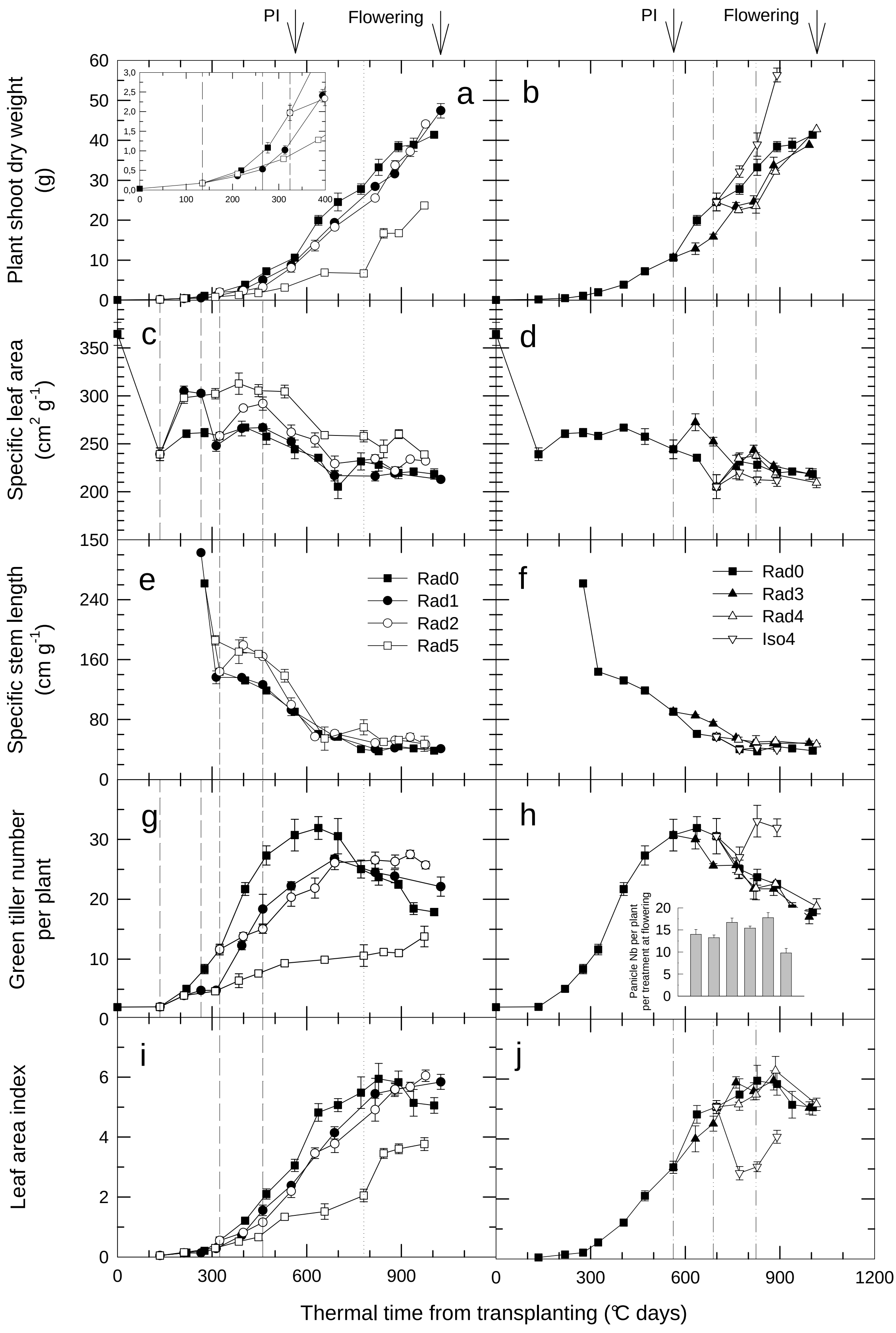


Fig. 7. Changes with TT from transplanting in plant shoot dry weight (SDW, a-b), SLA (leaf area divided by the leaf dry weight, c-d), SSL (stem length divided by stem dry weight, e-f), green tiller number per plant (g-h) and LAI (leaf area divided by plot area, i-j) for the different treatments. Arrows correspond to initiation of the panicle primordia (PI) and flowering. Insert in a is an enlargement of Rad1 and Rad2 SDW with TT. Insert in b shows the panicle number per plant per treatment at flowering. Same symbols as in Fig. 1 for the shading treatments plus Iso4 (∇) and same lines as Fig. 6 for the shading period. Verticals lines represent the standard error of the mean of the four replications.

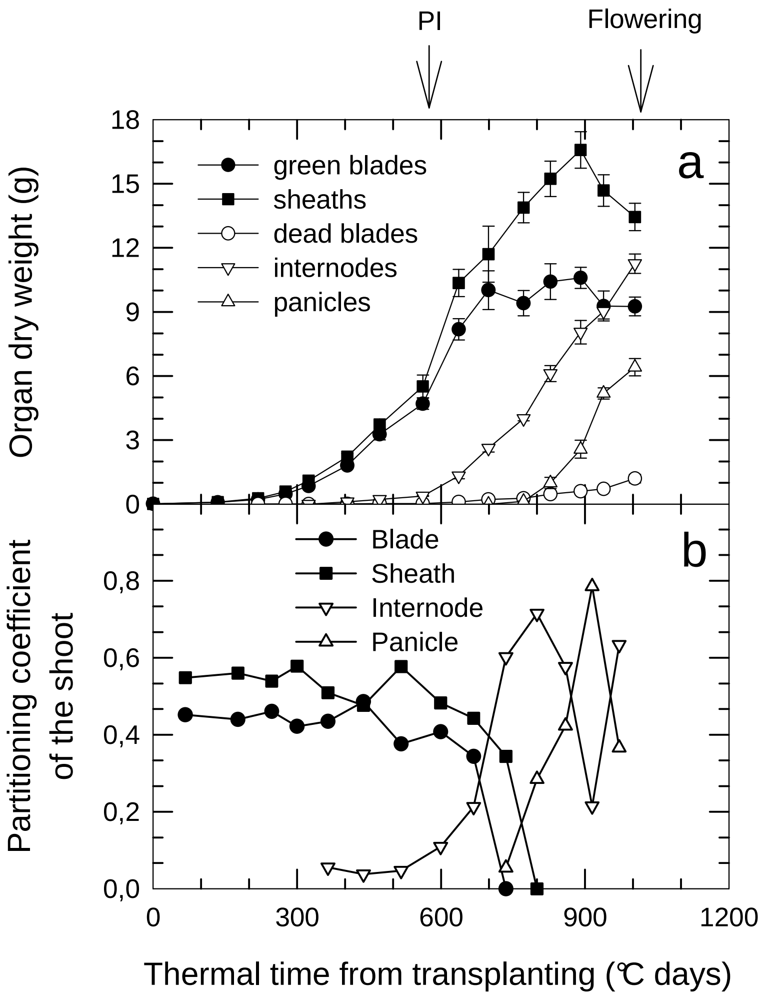


Fig. 8. Changes with TT in organ dry weight (a) and partitioning coefficient of the shoot (b) in Rad0 for green blades (●), sheaths (■), dead blades (○) , internodes (∇)and panicle (Δ).

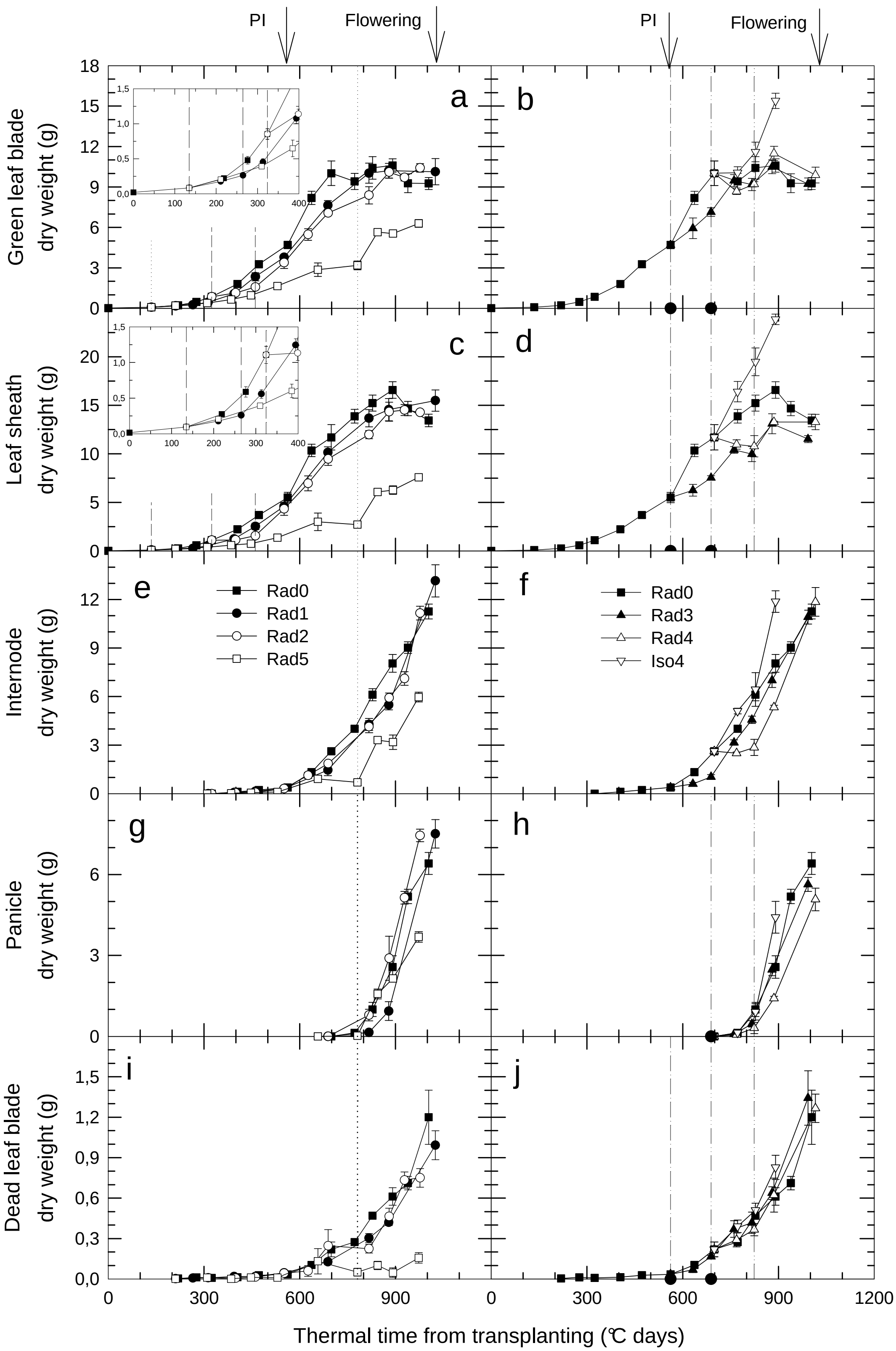


Fig. 9. Changes with TT in green leaf blade (a-b), leaf sheath (c-d), internodes (e-f), panicle (g-h) and dead leaf blade (i-j) dry weight for the different treatments. Arrows correspond to initiation of the panicle primordia (PI) and flowering. Insert in a is an enlargement of Rad1 and Rad2 green leaf blade dry weight with TT. Insert in c is an enlargement of Rad1 and Rad2 leaf sheath dry weight. Same symbols as in Fig. 7 for the treatments and same lines as Fig. 6 for the shading period. Verticals lines represent the standard error of the mean of the four replications.

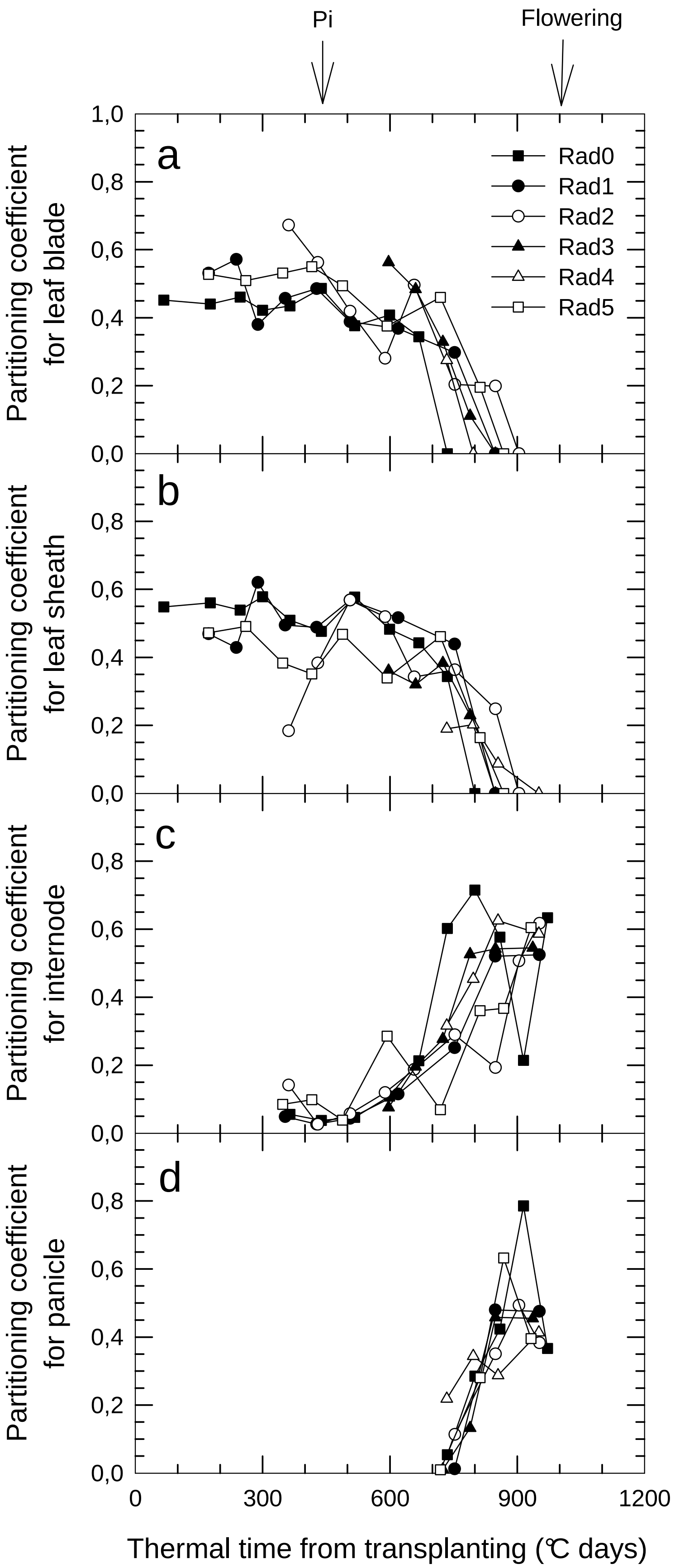


Fig. 10. Changes with TT in partitioning coefficient of the dry matter, calculated between each sampling date by dividing the increase in dry weight of each individual organ for the leaf blade (a), leaf sheath (b), internode (c) and panicle (d) in the different treatments. Arrows correspond to initiation of the panicle primordia (PI) and flowering

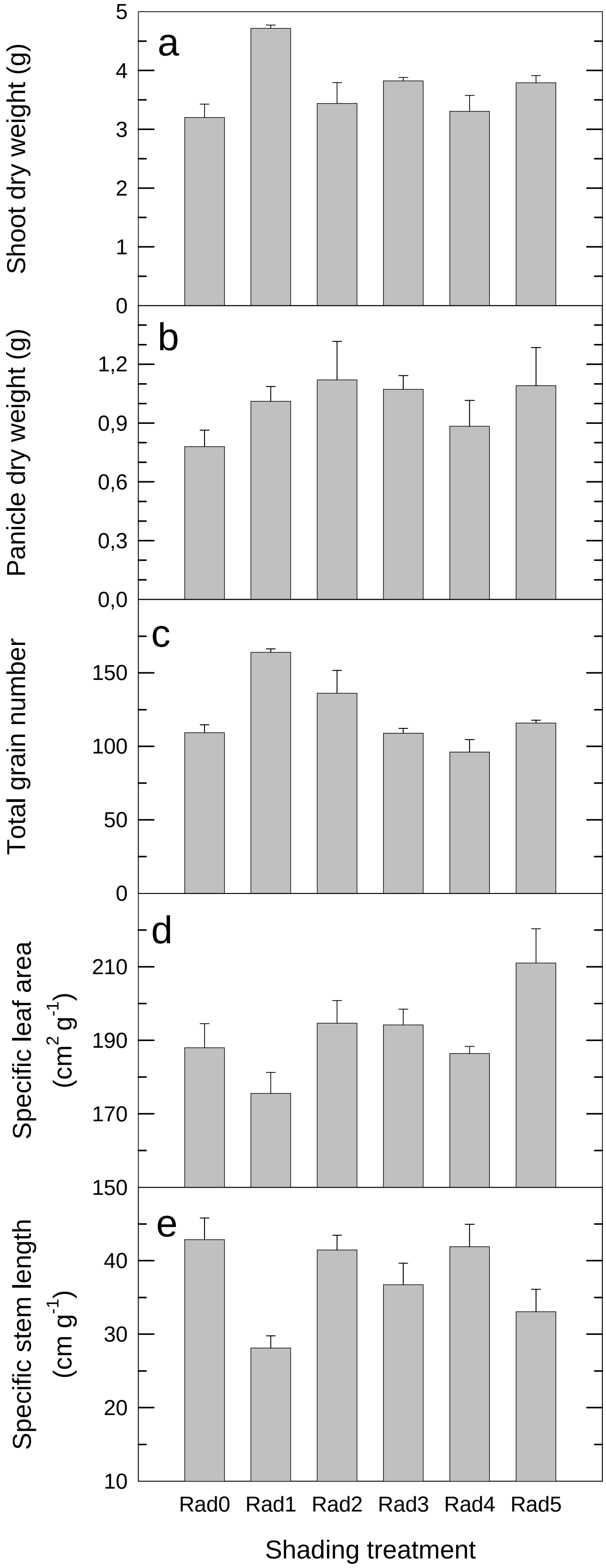


Fig. 11. Shoot (a), panicle (b) dry weight, total grain number (c), SLA (d) and SSL (e) of the main stem of the tag plants at 71 DAT for the different shading treatments. Verticals lines represent the standard error of the mean of five tag plants for four replications.